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DEDICATION

The Journal AMPHIPACIFICA is dedicated to the promotion of systematic biology and to the conservation of Earth's natural resources.

Cover design: Adapted from the title page of S. J. Holmes (1904). "Amphipod Crustaceans of the Expedition."
Harriman Alaska Expedition, pages 233-244.

Editorial Commentary . . .

Since completion of the first volume of *Amphipacifica* last spring, we have continued to receive expressions of both satisfaction and criticism concerning the quality of its content and editorial format. The commentary came from a wide spectrum of readers including: Mark Costello, Dublin, Ireland; Larry Hamblin, Romford, U. K.; Pierre Noel, Université de Paris, France; John Holsinger, Norfolk, VA.; Patricia McLaughlin, Anacortes, WA; Valerie MacDonald, West Saanich, Charles Low, Victoria, and Cas Lindsey, Vancouver, B. C. Jim Lowry, Australian Museum, Sydney, has pointed out a problem in one of early phoxocephalid plates that requires clarification. Niel Bruce, University of Copenhagen Museum, Denmark, has detected a number of editorial oversights in previous numbers that we have attempted to correct in this issue. Changes include a repositioning of the pagination and running head, more restricted use of underlining, oversize letters, and boldface type, and reduced use of abbreviations in the references. More careful attention has been given the alignment of type in parallel columns, and to consistency in labeling of illustrations. We welcome your further suggestions for improvement.

As the scope of the journal expands, we encourage exchange advertising with other journals of systematic biology, and with societies and agencies concerned with conservation of natural resources. We welcome submissions of medium to large systematic studies, and also shorter research papers and review articles that involve some aspect of aquatic biology and/or environmental concern. Although the journal emphasizes systematic research on aquatic invertebrate faunas of the North Pacific, as noted previously, publication criteria extend to other biomes (including terrestrial), other biotas (including vertebrates and fossil animals) and other regions (including the North Atlantic).

The first paper of this issue is a contribution to the reclassification of arthropods and arthropod-like animals, based on feeding and food-gathering mechanisms. Arthropod-like fossil animals of the Burgess Shale formation flourished in ancient Paleozoic seas some 520 million years ago. As a result of later orogenic processes, exquisitely preserved fossilized remains of these early crustacean and arachnid-like animals can be recovered from Middle Cambrian sedimentary rocks now situated at altitudes of about 1.5 km a.s.l. This study outlines possible phyletic relationships of known fossil species within two major groups of arthropods. These are defined as the uniantennates, including the aquatic Paleozoic trilobites and modern terrestrial arachnids, and the biantennates that encompass the mainly aquatic crustaceans, and modern terrestrial myriapod and hexapods. This enormous assemblage of joint-legged animals, comprising well over one million described species, fossil and recent, has been encompassed within a phyletic subdivision of only 9 superclasses and 29 classes. Quite remarkably, the total known Cambrian arthropod fauna of less than 100 fossil species, all aquatic, represents 6 of the superclasses and 14 of the classes, whereas the Recent arthropod fauna of over

one million described species, both aquatic and terrestrial, is contained in only 4 superclasses and 15 classes. Thus, the contention of Stephen J. Gould, set forth in his popular book "Wonderful Life" (1989), that the Cambrian fauna exhibited greater disparity (diversity at high taxonomic level) than at any other time in animal evolutionary history, finds strong support in the present analysis.

The second paper in the series treats the systematics and distributional ecology of North Pacific members of amphipod family Haustoriidae. Among macro-crustaceans, haustoriids are one of the most highly modified for a free-burrowing life style. The family is most diverse within the western North Atlantic region, especially along the sandy estuarine coastline of southeastern United States. However, one genus, *Eohaustorius*, has penetrated the North Pacific and is now nearly equally speciose along Asiatic and North American coastlines. Its subtidal species occur throughout the Pacific Rim region. However, intertidal species are apparently absent from corresponding Asiatic shores. There, winter conditions are severe, accompanied by sub-freezing temperature and shore icing; in summer, species of the competing fossorial talitroidean family Dogielinotidae dominate intertidally. Along corresponding North American Pacific sandy shores, however, winter conditions are relatively mild, shore icing is lacking and, in summer, only one species of intertidal dogielinotid occurs, and only along the open coast of Washington and Oregon states. Their infaunal densities, ease of collecting, and sensitivity to inimical substances, render certain species of *Eohaustorius* suitable for bioassay monitoring and testing of marine sediment toxicity.

The final paper is a continuation of a series of revisionary studies on the relatively primitive, benthic, gammaridean amphipod family Pleustidae. Member species are mainly micro-carnivores and commensals within marine communities of sessile invertebrates and attached plants. Subfamilies Parapleustinae, Pleusirinae, and Dactylopleustinae, investigated here, are almost wholly endemic to the North Pacific Rim region. Of the 32 known species combined, all but two occur nowhere else. The North Pacific marine shelf is characterized by long-term stability of associated biotic communities, and equable marine climates. These factors, presumably operating throughout the evolutionary development of the three pleustid subfamilies, are considered primary in dampening evolutionary thrust in other directions.

In summary, a remarkable feature of these three papers is the coincidental stratigraphic range of the marine animals encompassed, from the subtidal to the ocean abyss on the one hand, and from the supralittoral zone to high interior mountain slopes of British Columbia on the other.

With respect to the article on *Cadborosaurus* that appeared in the special supplementary issue of *Amphipacifica*, Vol. I, commentary pro and con has been received. A few excerpts are as follows: "You may have created some controversy with 'Caddy' but . . . you'll have provided some foundation for its recognition and study" (Dale Calder letter, June 19). "I was most impressed by . . . the paper on

AMPHIPACIFICA: PERSONAE NOVAE . . .



Marianne Wilkinson, B.A. (Eng), Associate Editor, has had a varied background in the field of communication and education. She has served as a high school teacher, news reporter, freelance writer, designer, and photographer. Following a four-year stint as a humour columnist, she became publisher and editor-in-chief of British Columbia's "Island Life" Magazine. Her avocational interests include writing, archeology, paleontology, and the outdoors, and is avid about flying.



Phillip M. Hoover, BSc., majored in biology at the University of Victoria, with emphasis on marine pollution biology and invertebrate taxonomy. During studies for the MSc degree in biology, he served as a teaching and research assistant in the laboratory of Dr. Derek V. Ellis with whom he co-authored studies on the impact and recovery of marine benthos in mine tailing wastes. Phil recently completed studies on the systematics of North American Pacific marine amphipods of families Haustoriidae, Amphilochidae, and Corophiidae, the first of which appears in this issue.

Production of this issue benefits greatly from the experienced editorial services of Tara Steigenberger, former assistant editor, Royal British Columbia Museum, Victoria.

Cadborosarus willsi . . . and I should like to distribute it among our subscribers (Jon Downes, Centre for Fortean Zoology, U. K.). " . . . You were right in publishing. Perhaps, some day, it might prevent another "Kermode" . . . (who make) hasty, often erroneous identifications" (Earl Godfrey, Ottawa). The popularized version entitled "*Cadborosaurus*, survivor from the deep", Horsdal & Schubart, publishers, Victoria, 134 pp., May, 1985, was "read with much interest" by several subscribers and friends, including Ian McTaggart Cowan, Victoria. Concerning this matter, the resignations of dissenting editorial associates of this journal, Craig Staude and Phil Lambert, have been accepted, regretfully. We are greatly indebted to Craig and Phil for their editorial help with previous regular issues of the journal, and wish them well in furthering their invertebrate research objectives.

The authors of the research paper on *Cadborosaurus* did not refer to a paper by Peter Scott and Robert Rines in *Nature*, 258: 466-468, 1975, in which the Loch Ness phenomenon was newly described as *Nessiteras rhombopteryx*. Their reconstruction, based on fixed demersal strobe flash

photographs of a partial body, neck and supposed hind flipper, portrays a thick-bodied, long-tailed animal with two pairs of large flippers. Such is quite unlike *Cadborosaurus willsi*, and the names are thus very probably not synonymous. Regretably, the Loch Ness specimen was not "in hand" at any time and, in our view, the photographs are not sufficiently distinct or complete to form the basis for a reasonably accurate interpretation of the animal's external morphology.

The difficulty of research here cannot be overestimated. Acquiring a further large specimen for detailed morphological study is very unlikely, but a small juvenile might again be captured alive and its behaviour studied in a marine aquarium. Despite several recent sightings in waters of the Saanich peninsula, May - August, 1995, neither video footage nor photographic "still" shots of this species at the water surface were obtained. However, these new sightings, made independently, some by two or more observers simultaneously, including one from a large deep freshwater lake not far from Victoria, further support the reality and recurring predictability of this large, anadromous, vertebrate species.

A CONTRIBUTION TO THE NATURAL CLASSIFICATION OF LOWER AND MIDDLE CAMBRIAN ARTHROPODS: FOOD-GATHERING AND FEEDING MECHANISMS.

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ABSTRACT

The classification of arthropods and arthropodlike invertebrates of Lower and Middle Cambrian strata is currently in a state of flux. Reanalysis of these early arthropods, however, indicates that a more widely acceptable basis for their natural classification might emphasize mechanisms of food gathering and feeding. Moreover, such mechanisms are usually readily determinable in both fossil and living specimens.

This study employs a relatively broad definition of the term "arthropod", and utilizes most higher classificatory names of the arthropod literature, but with reorganized emphasis. The views of Gould (1989) and Briggs et al. (1993) concerning high-level taxonomic diversity (disparity) of Lower and Middle Cambrian arthropods (*sensu* Walcott, 1912) are generally supported. However, these taxa have all been classified previously within accepted arthropod subcategories and none is considered new at the level of phylum or subphylum. Although the present analysis suggests plausible evolutionary pathways for food-gathering and feeding mechanisms in uniantennate (i.e., chelicerate) lineages, and possibly in biantennate (i.e., crustacean, myriapod and hexapod) arthropods, incorporation of these ideas within a suggested formal classification awaits broader acceptance among current workers.

INTRODUCTION

Arthropods are a major component of a fauna that, during the Cambrian Period, attained what has been described by Gould (1989) as a "maximum disparity of animal life". This concept, of broad morphological diversity at high taxonomic level (here defined as subclass or higher, or undetermined), has been questioned in detail by several (e.g., Ridley (1990, 1993; Briggs et al. (1992), but ably defended by Gould (1993) and Foot & Gould (1992). Thus, disparity of arthropods and arthropod-like forms does not appear to have been greater in Cambrian than in Recent times, whatever classifications are consulted or methodologies used (Wills et al., 1994). However, in proportion to the small number (<100) of Cambrian arthropod species recorded to date, from a half dozen or so major fossil sites world-wide, the percentage of high-level taxa that they represent is very much higher than that of comparable samples of Recent faunas. If considerations are restricted to aquatic faunas only, the percentage difference is even higher. Whatever the magnitude of these differences, however, the Cambrian Period can fairly be viewed as the period of arthropod evolutionary "explosion".

Cambrian arthropods are mostly unlike living representatives of the phylum, and therefore difficult to classify on existing natural bases. One of the richest arthropod assemblages, of about 35 species, has been described from Middle Cambrian Burgess Shale deposits in Yoho National Park, British Columbia (Conway Morris & Whittington, 1985). General and popularized treatments of that fauna, by Gould (1989) and Briggs et al. (1993), have summarized the original work of Charles Walcott (1912), and the subsequent careful descriptive treatments by Whittington (1971, 1975), Bruton (1981), Briggs (1979, 1981); Briggs & Whittington (1983, 1987), Collins (1987a,b), Collins & Rudkin (1981), Conway Morris (1986) and others. Their work has made

possible the present re-analysis of the early arthropod fauna for which the author feels most grateful.

Previous work has revealed a plethora of Cambrian taxonomic oddities several of which, according to Gould (1989), may require new higher classification, even at the level of phylum. Gould accepted, justifiably, the morphological interpretations of the aforementioned principal workers in this unfolding paleontological drama. Recent field work, especially in the Chengjiang region of southern China (Hou et al., 1991), and in Greenland (Conway Morris et al., 1987), has yielded many more important new taxa (e.g., by Hou, 1987 a, b; Hou & Bergstrom, 1991; Chen, et al. 1994). During his relatively brief two-year book-compilation period, Gould (1989) touched on the initial papers by Hou; however, he did not reference other pertinent works of group specialists (e.g. of Bergström, 1986; Schram, 1986; Dahl, 1984, 1987) that embody alternative and possibly more plausible classifications and evolutionary starting points, as suggested by the writer (Bousfield, 1987), for some of the major Burgess arthropod groups. Some reviewers (e.g., Fortey, 1989) have pointed to papers on cladistic classificatory methodology (e.g., Briggs & Fortey, 1989) that do provide credible, but not entirely correct, classifications of some of the enigmatic groups contributing to Gould's high disparity levels.

Delle Cave & Simonetta (1991) analyzed previous studies in a well illustrated and comprehensive account of early Paleozoic arthropods. They emphasized the importance of functionality, specially the the role of feeding appendages in the evolution of arthropod morphotypes. For the most part, their taxonomic groupings and evolutionary charts bring perceptive and cohesive insight to some mini-groups (e.g., trilobitomorpha, the *Sanctacaris* problem, and the Scanian larval stages), and stress the need for authors to name new taxa, whatever the later higher categories might be. However, they did not differentiate between food gathering and feeding (masticatory) roles and, as summarized in their

Table IV, apparently missed the significance of relationships within the Dicephalosomata and the overall relationships between anomalocarids and primitive trilobitomorph assemblages (which they did recognize) such as the Yohoiida and Leanchoiliida. Briggs et al (1993) continued with a conservative classification of early arthropods (p. 6) in which several previous higher taxa were not recognized and the anomalocarids omitted entirely. Whatever the merits or weaknesses of these various treatments, collectively they underscore the state of flux that presently characterizes early arthropod classification.

The purpose of this paper is to provide a classification that reflects more closely the actual degree of biological disparity and the major evolutionary themes within the Cambrian arthropod fauna. It also attempts to reveal, in more detail than previously, the relationship between form and food-gathering and feeding functions in selected Lower and Middle Cambrian arthropods and their descendent groups.

ACKNOWLEDGEMENTS

This study has taken place during a 10-year association with Dr Desmond E. Collins at the Royal Ontario Museum (ROM), Toronto, for whose tactful guidance and perceptive stimulus the writer is most grateful. Dr David Rudkin (ROM), Derek Briggs (University of Bristol, U.K.), Jan Bergström (Natural History Museum, Sweden), Jarmila Kukalova-Peck (Carleton University, Ottawa), Frederick R. Schram (Institute of Taxonomic Studies, Netherlands) and several others, have directly or indirectly provided helpful input to the text. Earlier drafts of the text have been helpfully reviewed by C. R. Harington and Stephen Cumbaa (Canadian Museum of Nature (CMN), Ottawa), Murray Copeland and T. E. Bolton (Geological Survey of Canada (GSC), Ottawa), and A. L. Hamilton (Biosystematics, Agriculture Canada). Lisa Bohach (Earth & Ocean Sciences, University of Victoria) has provided perceptive commentary and editorial services, and references not previously available to the author.

In the preparation of composite illustrations here I have been privileged to adapt, with warmest appreciation, the original text illustrations of D. E. G. Briggs, H. B. Whittington, D. E. Collins, F. R. Schram, X. Hou, L. Delle Cave, A. Simonetta, and several other primary sources.

In parallel to the present study, Professor Edward Laidlaw Smith, San Francisco, CA, has combined and collated previous arthropod categories in a detailed phyletic classification of arthropods (Atlas of Insect Anatomy, unpublished). Since this study has resulted in some similar classificatory conclusions, Dr Smith has generously permitted detailed reference to and use of updated non-insect arrangements in this text, for which I am most grateful.

SYSTEMATIC PREAMBLE

The term "arthropod" is here defined as an invertebrate having an externally segmented body that bears one or more pairs of jointed appendages. The body consists of head and

trunk regions, of which the latter may be tagmatized or subdivided into thorax and abdomen, mesosome and metasome, pygidium and/or telson, according to the taxonomic group. In primitive aquatic arthropods, the head always bears an acronal segment (first, or protocerebral somite) that is always pre-oral in position, having sensory organelles but no jointed limbs. The first true head segment (second or deutocerebral somite) is limb bearing, and usually pre-oral in active life stages. The head may also encompass up to five (rarely six) additional limb-bearing segments, the first of which (third or tritocerebral somite) may appear pre-oral in position. The post-oral appendages of head and trunk are primitively or embryologically biramous, the segments of which are externally chitinized, sclerotized or mineralized. The inner ramus is usually locomotory, food gathering or masticatory, and the outer ramus usually respiratory in function. Growth proceeds by moulting of the ectoderm (ecdysis). Following Bergström (1986, 1987) and Chen et al. (1994), true arthropods here embrace the primitive Cambrian dicephalosomatid genera *Anomalocaris*, *Opabinia*, *Cassubia* and close relatives. However, contrary to the views of Snodgrass (1956) and Manton (1977), true arthropods do not include the Tardigrada nor the Onychophora in which the body is not externally segmented and the post-oral limbs, although dactylate (clawed), are not jointed nor biramous.

The Middle Cambrian macro-arthropod fauna is characterized by a high percentage of primitive body forms that, superficially, appear to be intermediate between true worms (phylum Annelida) and higher groups of aquatic arthropods such as the Chelicerata and Crustacea. Paradoxically perhaps, some of these early forms (e.g., *Opabinia*) show a remarkably high degree of specialization of body form and function that tends to mask their true phyletic affinities. In adult stages of some primitive modern arthropods (e.g., Remipedia) and larval stages of cirripedes, phosphatocopine ostracods and skaracarids, the acronal segment bears conspicuous frontal organs or frontal filaments of presumed sensory function, and/or a median naupliar eye (Schram, 1986). The acronal somite is especially well developed in skaracarid crustacean larvae (e.g., *Martinssonina* Müller & Walossek, 1986). However, in arachnids, myriapods and hexopods, the acron is considered embryonic and fused with the second head somite in active life stages (Savory, 1964).

The first true head segment (second somite) of arthropods bears one pair of limbs, of 1-14 basic segments, that is embryonically uniramous and pre-oral. These limbs may be stout, the segments spinose or toothed, or apically pincer-like and raptorial in function, as in chelicerates and their presumed precursors. However, more often they are filamentous and sensory in function, as in the "antennae" of trilobites, and the antennules of crustaceans and their presumed ancestors, and marrellomorphs. In some Cambrian arthropods (e.g., *Leanchoilia*), the appendage appears distally multi-flagellate. In higher crustaceans (Malacostraca), the antennules are often secondarily biramous (e.g., in Eumalacostraca), and occasionally triramous (in Stomatopoda). In myriapods and insects, the antennae are

uniramous, filamentous and sensory. In no instance, however, are these appendages gnathobasic.

The third head somite (rarely lacking except in a few Cambrian species such as *Opabinia* and *Sidneyia*) bears a pair of limbs homologous with the antennae of crustaceans and early biantennate arthropods. These limbs, homologous also with the pedipalps of chelicerates and pycnogonids, may be uniramous or, as in the intercalary (supralingual) segment of myriapods and hexapods, vestigial or essentially lacking. In primitive arachnids and early precursors, and in larval stages of crustaceans, limbs of the third head somite are masticatory as well as locomotory and/or respiratory in function. Thus, as will be demonstrated in Cambrian aquatic arthropods (below), the evolutionary trend in functioning of the first two pairs of appendages in arthropods progresses from food gathering and mastication, to food sensing and tactility.

The head segment and limb homologies employed in this study, and suggested classification (pp. 23-27), conform with classical concepts of arthropod head structure, innervation and embryology (e.g., of Borradaile & Potts, 1941; Savory, 1964; Bergström, 1979). Kukalova-Peck (1987) and Smith (1990) have fused the acronal segment of hexapods with the labrum to form the clypeolabral, or first (protocerebral) somite which, in Upper Carboniferous monurans, appears basolaterally segmented. The second head somite remains the antennal (deutocerebral) somite, homologous with the antennular somite of crustaceans. However, Smith (loc. cit.) has suggested that the chelicerae of arachnids originate on the third (tritocerebral, supralingual) somite, and the pedipalps on the fourth or mandibular segment, resulting in eight prosomal somites, one more than the normal maximum recognized by all other authors.

In Cambrian arthropods, the anterior portion of the gut is typically deflexed and the mouth usually opens ventrally on the head. In a few groups, however, (e.g., *Jianfengia*, *Sanctacaris*) the mouth appears to open apically or frontally (Hou, 1987a, Briggs & Collins, 1988). Body segmentation may not always be externally visible, especially in larval forms, or in highly modified adults (e.g., some internal parasites). Paired limbs of the trunk are primarily biramous, but may be secondarily uniramous. The branches may be variously modified, unsegmented, or lacking (e.g., in early growth stages and in adults of various taxonomic groups). Thus, in a biramous limb, the outer branch may be lightly chitinized and flaplike (unsegmented) in swimming forms or, when the outer is respiratory in function, the inner branch may be fully segmented, leglike, and heavily calcified or mineralized, especially in heavy bodied benthic forms. As noted above, some post-oral paired appendages may be gnathobasic wherein the coxa and/or adjacent segments are medially toothed, or the entire limb reduced and modified as a specialized mouthpart (e.g., mandible or maxilla). Such feeding appendages are tagmatized as part of the cephalon.

Morphological differences between major groups of arthropods are fully as great as between accepted subphyla

and classes within other major phyla (e.g., as between chitons and cephalopods within phylum Mollusca). In Lower Cambrian to Lower Ordovician times (530-500 m.y.b.p.), major groups of arthropods having modern representatives (e.g., Chelicerata, Crustacea) were then in what might be termed a primordial or early state of evolution or, in the case of Myriapoda and Hexapoda, unrecognized as such. Thus, true crustaceans were represented in the Cambrian fossil record only by the Maxillopoda (Ostracoda, Cirripedia, and skaracarid larval forms) (see Schram, 1986 in part; Dahl 1984, 1987). Members of the Aglaspida (Upper Cambrian) were considered by Bergström (1979) to be early chelicerates but Briggs et al. (1978) demonstrated the filamentous nature of the "chelicerae" and removed the Aglaspida from the merostomes. The earliest chelicerates are *Chasmatspis*, or perhaps *Triopus*, from the Lower Ordovician (Fig. 8). Other major arthropod groups (e.g. Myriapoda, Hexapoda) were recognizable in late Silurian and early Devonian times, when freshwater and terrestrial fossils deposits were first identified.

PREVIOUS CLASSIFICATIONS

Several different classifications of Cambrian macroarthropods have been proposed, four of which are presented in Table I. The 17 sample species listed here were classified initially by Walcott (1912) who "shoehorned" them (*vide* Gould, 1989) into a relatively few existing crustacean and arachnid subcategories (Column 1). Over the next 75 years the species were classified variously by Störmer (1959), Sharov (1966) and Bergström (1979), and incorporated by Edward Laidlaw Smith in a forthcoming "Atlas of the Insecta", communicated to the writer, with kind permission, for comparative purposes here (Column 4). Despite previous designations, Gould (1989) regarded these forms as highly distinctive, belonging to two new phyla; 12 unique arthropods; one chelicerate arthropod; one trilobite; and one malacost-racan (Column 2). Briggs et al. (1993) had retreated into a somewhat similar conservative listing of Cambrian arthropods, a list that did not include *Anomalocaris*, *Opabinia*, and other dicephalosomatid forms (Column 3). The E. L. Smith listing (Column 4) would place 15 of Gould's new or unique taxa within long-established classes of crustaceans, trilobitoids, protochelicerates, and chelicerates, five of them more or less within Walcott's original categories. However, as we may note in the following text, Smith's placement of *Marrella* and *Branchiocaris* within the protochelicerates, and *Odaraia* and *Canadaspis* within the Crustacea, is interpreted otherwise here.

Mechanisms of food-gathering and feeding.

In assessing the overall legitimacy of these classifications, we might conclude that, under the circumstances of the relatively limited systematic knowledge of his day, Charles Walcott was remarkably perceptive in much of his classification. Although the reticence of Gould and Briggs to refine

TABLE I. THE CLASSIFICATORY STATUS OF SOME BURGESS SHALE FOSSIL GENERA

Genus Name	Higher category by Author			
	Walcott (1912)	Gould (1989)	Briggs et al (1993)	E.L.Smith ("Atlas" prep)*
<i>Marrella</i> (Walc.)	near Trilobita	unique	Arthropod	Protochelicerata Størmer, 1944
		arthropod	(primitive)	CL. Marrellidea Walcott 1912
<i>Yohoia</i> (Walc.)	branchiopod	unique	Arthropod	Protochelicerata Størmer, 1944
	crustacean	arthropod	(other)	CL. Yohoiidea Henriksen 1928
<i>Opabinia</i> (Walc.)	branchiopod	new	Unassigned	Protochelicerata Størmer, 1944
	crustacean	phylum	Invertebrate	CL. Probosciferidea Sharov 1966
<i>Burgessia</i> (Walc.)	branchiopod	unique	Arthropod	Trilobitoidea Størmer, 1955
	crustacean	arthropod	(other)	O. Nectaspida Raymond, 1920
<i>Branchiocaris</i> (Walc.)	malacostracan	unique	Arthropod	Protochelicerata Størmer 1944
	crustacean	arthropod	(primitive)	CL. Branchicaridea
<i>Canadaspis</i> (Walc.)	phyllocaridan	malac-	Crustacea	Crustacea Pennant 1777
	crustacean	ostracan		CL. Branchiopoda Latr. 1817
<i>Naraoia</i> (Walc.)	branchiopod	soft-bodied	Trilobita	Trilobitoidea Størmer, 1955
	crustacean	trilobite		O. Nectaspida Raymond 1920
<i>Odaraia</i> (Walc.)	malacostracan	unique	Crustacea	Crustacea Pennant 1777
		arthropod		CL. Branchiopoda Latreille, 1817
<i>Sidneyia</i> (Walc.)	merostome	unique	Arthropod	Protochelicerata Størmer 1944
		arthropod	(other)	CL. Sidneyiidea Walcott, 1912
<i>Molaria</i> (Walc.)	merostome	unique	Arthropod	Trilobitoidea Størmer, 1955
		arthropod	(other)	<i>incertae sedis</i>
<i>Habelia</i> (Walc.)	merostome	unique	Arthropod	Trilobitoidea Størmer, 1955
		arthropod	(other)	<i>incertae sedis</i>
<i>Actaeus</i> (Walc.)	unknown	unique	Arthropod	Protochelicerata Størmer, 1944
		arthropod	(other)	CL. Leancholiidea Raymond!
<i>Alalcomanaeus</i> (W.)	unknown	unique	Arthropod	Protochelicerata Størmer, 1944
		arthropod	(other)	CL. Leancholiidea Raymond!
<i>Emeraldella</i> (Walc.)	merostome	unique	Arthropod	Protochelicerata Størmer, 1944
		arthropod	(other)	CL. Emeraldellidea Raymond!
<i>Leancholia</i> (Walc.)	branchiopod	unique	Arthropod	Protochelicerata Størmer, 1944
	crustacean	arthropod	(other)	CL. Leancholiidea Raymond!
<i>Sanctacaris</i> (Briggs & Collins)	N/A	chelicerate	Chelicerata	Chelicerata Heymons 1901
			arthropod	Arachnida Lamarck, 1801
<i>Anomalocaris</i> (Walc.)	branchiopod	new	Unassigned	Protochelicerata Størmer, 1944
+ <i>Laggania</i>		phylum	Invertebrate	CL. Anomalocaridea Raymond!
+ <i>Peytoia</i>				
+ appendage F	* Selected names with permission of E. L. Smith (references not detailed here); ! - Raymond, 1935.			

the classification with new terminology is to some extent justified, Smith's listing of previous formal categories indicates that their reticence does not provide a helpful solution to the problem. The need seems greatest for more careful and more rigorous definition of existing categories, based on principles of functional morphology where possible, and a resort to new categories when existing or redefined categories prove inadequate. As Gould (per Schram, 1990) reminds us, errors and oversights of the past are part of the process of getting the probably correct answer, and so provide a prime stimulus for the present undertaking.

Gould (1989) noted that previous workers on Cambrian arthropods seemed reasonably confident of their classification of the most primitive forms, e.g., the Onychophora, and the presumably most advanced major taxon, the Trilobita.

However, they seemed less certain of other arthropods variously attributed to the Crustacea (ie. Canadaspidida, Branchiocarida) or having only general similarities with the Trilobita. The greatest difficulties were encountered with forms having both annelid-like and arthropod-like features (e.g. *Anomalocaris*, *Opabinia*). Charles Walcott (1912) utilized subcategories of extant arthropod groups (e.g., Branchiopoda, Ostracoda + Merostomata). Størmer (1944, 1959) proposed new "catch-all" categories (e.g., Trilobitoidea) for many enigmatic forms. These classifications utilized standard character states such as body tagmatization, number of paired head (or head shield) appendages, types of appendages (biramous, gnathobasic, gill-like) and larval biology, to the limit of existing knowledge, but did not emphasize functionality or possible behavioural significance.

Bergström (1979, et seq.) employed the term "Schizoramia" to encompass all Trilobitomorpha (Trilobita, Merostomatoidea, and Chelicerata). These are characterized by primitively biramous trunk limbs of which the endopod is gnathobasic, and the exopod bears lamellar spines. The enigmatic genus *Emeraldella*, having gnathobasic post-oral legs, was included here, as well as the Marrellomorpha, but the latter group primarily lacks gnathobasic limbs. The Pycnogonida (Pantopoda) was not related to any particular arthropod group. Commendably, Bergström relegated *Opabinia* and *Anomalocaris* to the status of a "pre-arthropod" stock, but later (1986, 1987) decided they were indeed arthropods, a view now firmly supported by the recent work of Chen *et al* (1994). However, Bergström employed the term Uniramia to encompass both the soft-bodied, externally annulated onychophorans, and the hard-bodied, externally segmented myriapods and hexapods having whole-limb jaws. This concept is now proving flawed and untenable as a category of natural classification (see Kukalova-Peck, 1992). Onychophorans, early forms of which did exist in Cambrian seas, resemble the Tardigrada in having shaft-like, primitively uniramous limbs and pharyngeal teeth or spines, whereas myriapods and insects have segmented, primitively biramous limbs, and mouthparts modified from biramous limbs. Furthermore, Bergström's doubts that biramous and mandibulate crustaceans arose from the same gnathobasic limb stock as hexapods are not supported here nor by some other workers (e.g., Kukalova-Peck, 1987). Imperfect fossilization has so far prevented determination of the precise nature of locomotory limbs of dicephalosomatids. However, such is not here considered a major impediment to phyletic implications of the better preserved, clearly "arthropodized" feeding appendages of the head region, nor overall relationships with confirmed early biramous arthropod groups.

In assessing the impact of feeding processes on the evolution of body form in arthropods, a definition of terms is prerequisite. The entire feeding process encompasses food-gathering and food-consumption mechanisms. The food-gathering mechanism is the process by which food items are entrapped and brought to the mouth region. The food-consumption (feeding) mechanism is the process of mastication, the external means by which food items are rendered suitable for entry into the digestive tract proper.

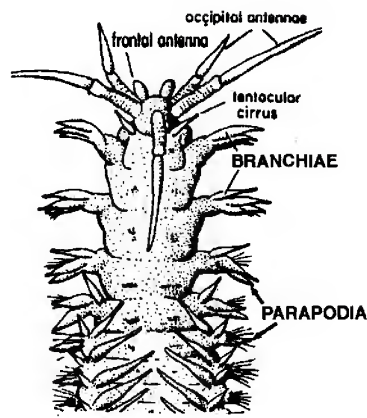
Basic types of feeding processes of arthropods and their presumed antecedents are illustrated in Fig. 1. In errant polychaete worms (e.g., *Nereis*, *Neathes*), a taxonomic group "classically" presumed ancestral to the arthropods, the head consists of a prostomium and usually a peristomial segment bearing food-sensing tentacles. No paired limbs, segmented or otherwise, are involved in food gathering or in food mastication; these processes are entirely pharyngeal (Fig. 1A). The mechanism consists of an eversible pharyngeal proboscis, the everted distal end of which is armed with strong teeth or "jaws" by means of which the food material (prey organism) is captured and killed. As the proboscis

retracts, it re-inverts, taking in the prey and partly macerating it by means of other teeth lining the pharynx wall. The food is then passed rearward to the digestive gut proper. No true arthropods conform with this category.

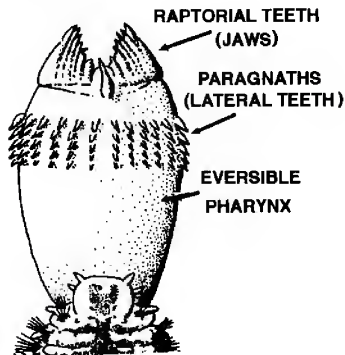
In very primitive uniantennate arthropods, (e.g., *Anomalocaris*, Fig. 1B.1), food is gathered by the large, spinose and multi-segmented, pre-oral paired appendages. These capture and transfer prey organisms posteriorly to the mouth region that opens immediately behind the first true head segment. The actual feeding mechanism, however, remains entirely pharyngeal; no paired mouthparts or leg gnathobases are present, although in the related *Opabinia regalis* (Fig. 1B.2), some prey items may be partly macerated by the pre-oral clawed appendage. In the anomalocarids, food is initially macerated by means of peribuccal teeth, and/or stout teeth or spines lining the anterior walls of the pharynx, as in some polychaetes. This feeding process is analogous, or perhaps even homologous, to mechanisms elsewhere among living arthropods in the pycnogonids, and among other invertebrates in the cephalopod molluscs (Borradaile & Potts, 1941). In cephalopods, the "head-foot" appendages (tentacles) grip, but do not masticate, the prey by means of specialized suckers, rather than spines; modified anterior pharyngeal teeth, the horny beaks, and smaller radular teeth masticate the prey items just inside the mouth entrance.

In more advanced uniantennates (e.g. in chelicerates, Fig. 1C), food gathering is also the prime function of post-oral head (prosomal) appendages, and/or the cheliform pair of pre-oral appendages. In primitive aquatic chelicerates (e.g., merostomes), the food is first macerated externally by means of a grinding action of the gnathobasic coxae of the paired head and/or trunk appendages. In more advanced terrestrial arachnids that secondarily lack leg gnathobases, the killing bite and maceration of the prey is performed by the distally clawed first post-oral appendages, the pedipalps and/or the pre-oral chelicerae (Savory, 1964).

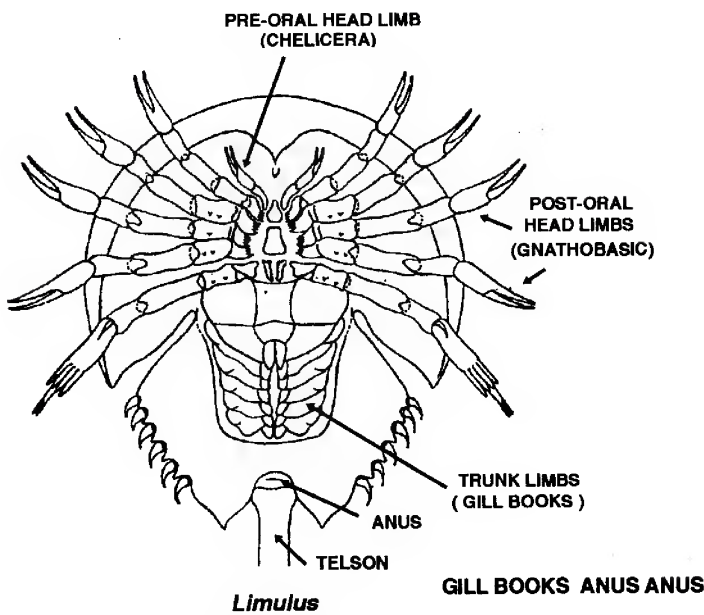
Within advanced biantennate (mandibulate) arthropods (e.g., malacostracan crustaceans, Fig. 1D), the pre-oral and first post-oral appendages are flagellar and food-sensing. Food is gathered mainly by the anterior trunk (thoracic) limbs. Swimming, and often respiratory functions may be relegated to the posterior trunk (abdominal) limbs. Food is macerated by specialized post-oral limbs of the head region, the mandibulate mouthparts. Other branches or lobes of post-oral head appendages may serve in locomotion, and/or respiration, especially in adults of more primitive groups (e.g., cephalocaridans) and in larval stages of advanced forms. Food mastication may also become the primary function of one to three pairs of anterior trunk limbs, serving as maxillipeds (e.g., in Decapoda), or as gnathopods (e.g., in Amphipoda). In their larval stages (e.g., nauplii, metanauplii) the biramous first post-oral appendage (antenna 2) usually retains a function in food gathering and mastication, as well as locomotion (Schram, 1986).



Nereis

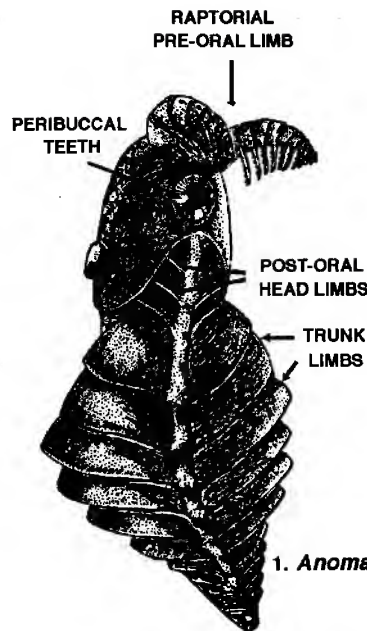


A. PHARYNGEAL

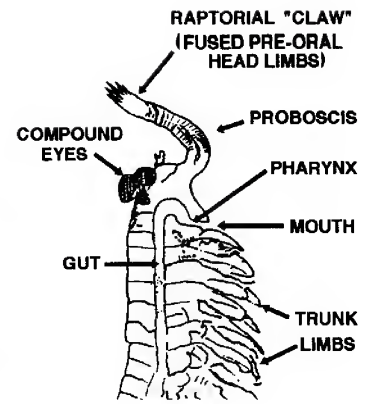


Limulus

C. CHELICERATE PRE-ORAL, GNATHOBASIC POST-ORAL

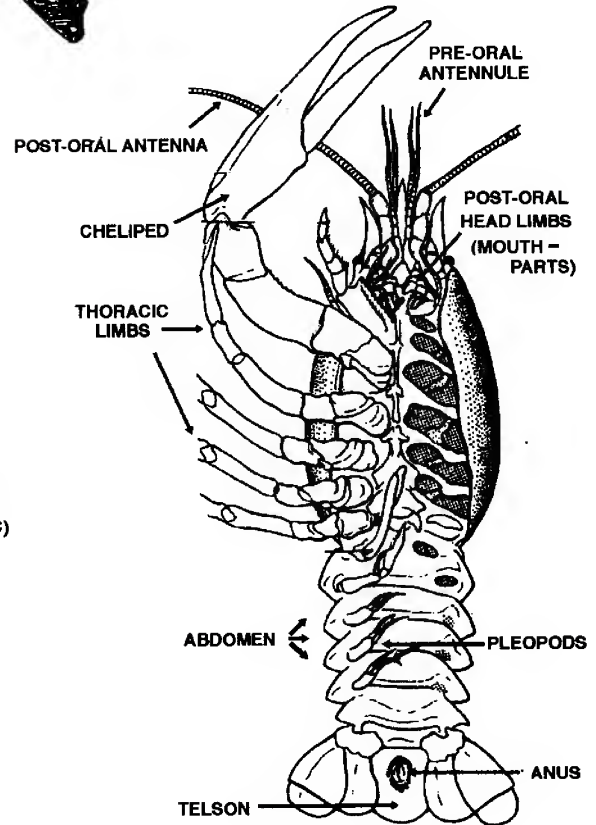


1. *Anomalocaris*



2. *Opabinia*

B. RAPTORIAL PRE-ORAL & PHARYNGEAL



Orconectes

D. ANTENNAL PRE-ORAL, MANDIBULATE POST-ORAL

FIG. 1. BASIC TYPES OF FOOD-GATHERING AND FEEDING MECHANISMS IN AQUATIC ARTHROPODS. A. Polychaete (ancestral). B. Primitive uniantennate arthropod. C. Advanced uniantennate arthropod D. Advanced biantennate arthropod

**TABLE II. SELECTED GENERA OF CAMBRIAN UNIANTENNATE ARTHROPODS
CATEGORIZED BY FOOD-GATHERING AND FEEDING MECHANISMS**

SEGMENTED LIMBS LACKING I.	SEGMENTED PRE- AND POST-ORAL LIMBS			
	II. PRE-ORAL LIMBS RAPTORIAL	III PRE-ORAL LIMBS TRANSITIONAL	IV. PRE-ORAL LIMBS FILAMENTOUS	V. PRE-ORAL LIMBS CHELICERATE
PHARYNGEAL MASTICATION	PHARYNGEAL MASTICATION	TRANSITIONAL PHARYNGEAL MASTICATION	GNATHOBASIC MASTICATION	GNATHOBASIC MASTICATION
POLYCHAETA	ENDOPODS LOBATE OR SMOOTH <i>Anomalocaris</i>	ENDOPODS SPINOSE <i>Leanchoilia</i>	<i>Sidneyia</i> <i>Burgessia</i>	<i>Chasmataspis</i>
TARDIGRADA	<i>Laggania</i>	<i>Acanthomeridion</i>	<i>Molaria</i>	† MEROSTOMATA
ONYCHOPHORA	<i>Opabinia</i>	<i>Actaeus</i>	<i>Habelia</i>	† EURYPTERIDA
<i>Hallucigenia</i>	† <i>Tullimonstrum</i>	<i>Alalcomanaeus</i>	<i>Tegopelte</i>	† SCORPIONIDA
<i>Aysheaia</i>	<i>Cassubia</i>		<i>Naraola</i>	
	<i>Jianfengia</i>		TRILOBITA	
	<i>Yoholia</i>		<i>Sanctacaris</i>	
			<i>Emeraldella</i>	
			<i>Aglaaspis</i>	

† Ordovician and later

? Head limbs not gnathobasic

Selected uniantennate arthropods of the early Paleozoic are grouped according to categories of food gathering and feeding outlined in Table II. As noted previously, unassisted pharyngeal feeding typifies polychaetes and pararthropods such as the tardigrades and onychophorans (Column I). The dicephalosomatid arthropods (Column II) utilize only raptorial pre-oral appendages in food gathering and/or preliminary food mastication. They feed in an essentially similar pharyngeal manner, except that the mouth opening is deflexed ventrally in anomalocarids and proboscoideans, and opens anteriorly (or nearly so) in *Yohiida* (Hou, 1987a). In primitive trilobitomorphs, the *Leanchoiliidacea* (Column III), the post-oral head and trunk limbs appear capable of capturing and holding food items but feeding is still essentially pharyngeal. In the advanced species *Alalcomanaeus*, post-oral limbs are essentially gnathobasic (Delle Cave & Simonetta, 1991). In advanced trilobitoideans, including *Sidneyia*, the *Burgessiida*, trilobites, *Emeraldellida* and *Sanctacarina* (Column IV), the pre-oral appendages become essentially singly filamentous in form and presumably chemosensory and thigmotactic in function. The post-oral head and trunk limbs become fully gnathobasic (although remaining biramous) and presumably assisted in both food capture and food mastication. The chelicerates are a final stage in the uniantennate feeding series (Column V). The raptorial pre-oral limbs are reduced to two to four segmented chelicerae, and the post-oral head limbs are fully gnathobasic and essentially uniramous. Both types of head appendages may assist in food gathering and food maceration, especially in the terrestrial arachnid subgroups. The anterior post-oral trunk limbs are essentially uniramous; the endopod is lost, but the exopod remains functional in respiration.

This tabular arrangement of taxa according to feeding style parallels an increasing evolutionary sophistication of head and trunk segmentation, and form and function of their appendages as detailed in pages 11-14. It also matches the

fossil track record of the uniantennate groups (Table V, p. 28). Thus, the most primitive feeding styles, as in the dicephalosomatids, persisted little beyond the Cambrian Period and not beyond the Palaeozoic Era. By contrast, the most advanced uniantennate feeding types expanded into the chelicerate taxa of Ordovician and later periods, including the remarkably diverse terrestrial arachnids of Tertiary and Recent times.

Evolution of Post-oral Limb Morphology

The changing structure of the post-oral head and trunk appendages of uniantennate arthropods is depicted in greater detail in Figure 2. Within the Dicephalosomatida, the Anomalocarida and Probosciferida were equipped with pairs of closely approximated paddlelike plates on each side, not clearly joined at the base, and perhaps not technically, even if functionally, forming a biramous limb. The upper plate (in *Opabinia*, Fig. 2B, C) was fringed with lateral lamellae, presumably respiratory in function. The head of *Opabinia* (2B, C; 7C.1) lacked post-oral plates, but the three pairs of post-oral head plates in *Anomalocaris* (Fig. 2A) are considered homologous with the trunk plates. In *Cassubia* (Fig. 3), considered here (and by Smith, "Atlas" unpubl.) as a benthic anomalocarid with relatively short stout pre-oral limbs, the head may be two segmented. Trace elements alongside the trunk may be ambulatory endopods of the posterior head and/or anterior trunk segments. In *Yohiida*, including the multi-segmented *Jianfengia* from the Lower Cambrian of China (Fig. 7G), the head bore 3 pairs of post-oral appendages of which the endopod was 7-segmented, cylindrical, and presumably ambulatory. The limbs were not demonstrably gnathobasic, but the ectoderm was sclerotized or mineralized, with a gill-like exopod, much as in a trunk limb of the biantennate genus *Marrella* (Fig. 2D). An exopod was present and foliaceous in head limbs of the elongate *Jianfengia*

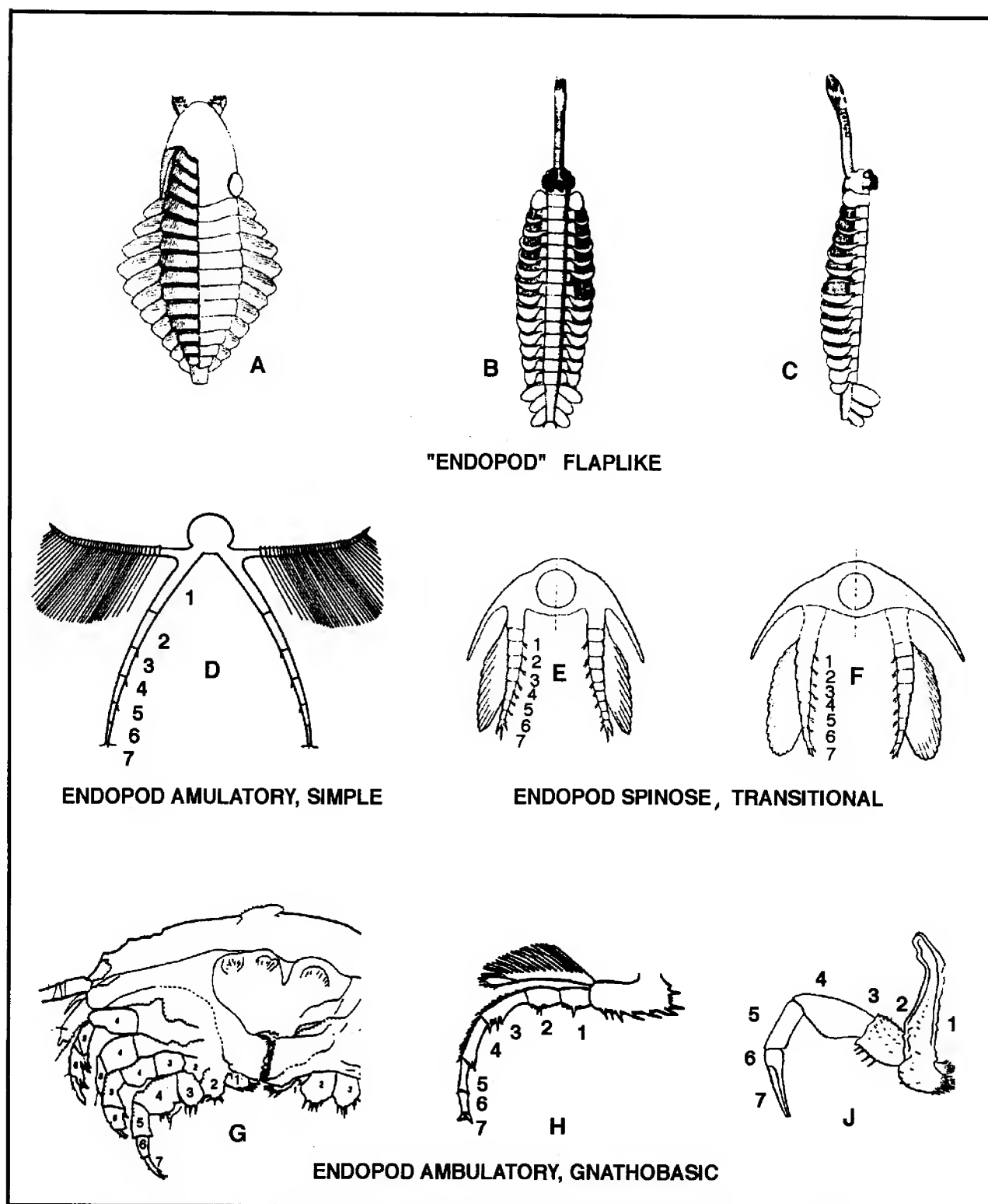


FIG. 2. BILOBATE AND BIRAMOUS POST-ORAL (HEAD AND TRUNK) LIMBS OF PRIMITIVE ARTHROPODS OF THE EARLY PALEOZOIC ERA.

A. *Anomalocaris* (section) B. *Opabinia* (dorsal) C. *Opabinia* (lateral)
 D. *Marrella* (trunk section) E. *Leancoilia* (post-oral section) F. *L.* (trunk section)
 G. *Sidneyia* (post-oral section) H. *Triarthrus* (trunk limb) J. *Limulus* (leg 2)

but apparently lacking in those of the relatively short-bodied and more advanced *Yohoia*. Trunk limb exopods were broad, as in the trilobitomorph *Leancoilia* (Fig. 2E, F), and margins setose, as in *Sanctacaris* (Fig. 6). At least the first pair, and possibly up to 10 pairs, of anterior trunk limbs bore a cylindrical ambulatory endopod.

Within the primitive transitional trilobitomorphs, including the *Leancoiliidae* and *Actaeida* (Figs. 2E, F), the 3 pairs of post-oral head limbs, and all trunk limbs, developed strong spines on the inner margins of the segments of the endopod. The spines were presumably used in grasping and holding prey organisms, much in the manner of the thoracic leg spines of eusirid amphipods and adult dragonflies. In more advanced groups of trilobitoids, the post-oral limbs of head and trunk became fully gnathobasic, in which strong teeth or spinose processes developed on the proximal (coxal and basal segments) of the endopod. The distal claws of the endopods functioned in seizing, and the gnathobases in killing and masticating, prey items prior to transfer to the mouth proper. In *Sidneyia* (Fig. 5D), the head lacked post-oral limbs but the anterior four pair of trunk limbs were strongly gnathobasic and uniramous, the remaining trunk limbs biramous. In *Burgessiida* and in the *Trilobita* proper (Fig. 2H), the 3 pairs of post-oral head limbs remained fully biramous and multifunctional. The outer ramus bore numerous respiratory lamellar spines. In the *Emeraldellida*, including *Emeraldella* (Figs. 6E, 7M) and *Sanctacaris* (Figs. 6, 7L) the anterior two trunk segments became fused to the head, resulting in 5 pairs of post-oral head appendages. As the locomotory and respiratory functions decreased and raptorial and masticatory functions of the head limbs increased, the endopods became more powerfully raptorial and gnathobasic, whereas the exopods became vestigial, as in *Sanctacaris*. In the aquatic chelicerates, the merostomes (e.g. *Limulus*, Fig. 2J), the head region similarly bear five pairs of strongly gnathobasic, ambulatory and essentially uniramous limbs. However, the pre-oral limbs of merostomes are chelicerate, not filamentous, and derived from very different ancestral uniantennates (see page 12). In all but the most primitive aquatic merostomes, the trunk endopods lost their ambulatory function and disappeared, whereas the anterior pairs of trunk exopods remained functional in the form of book gills and, in terrestrial derivatives, book lungs.

In the above evolutionary sequences, the development of gnathobasic limbs may have been a consequence of improved efficiency in exploiting, as food, hard-shelled prey living in soft bottom sediments. The feeding style of *Limulus* still follows this original primitive pattern.

Evolution of Food-Gathering Appendages

Within uniantennate arthropods, the morphological and functional forms of pre-oral food-gathering and food-sensing appendages may be linked in possible evolutionary pathways (Fig. 3). The presumed ancestral form of this cephalopod-style food-gathering mechanism is the large multi-segmented raptorial form typical of species of *Anomalo-*

caris (Figs. 3A, D). Despite anomalies of fossil limb preservation, the primary plane of motion is presumed to be essentially vertical. The paired limbs combined, nearly in parallel, to form a raptorial basket in which prey organs were captured and killed by the daggerlike posterior (inner) marginal spines (Collins, 1987). The food items were then transferred posteriorly, by deflexion and retraction of limbs, to the masticatory buccopharyngeal teeth of the mouth region. This plane of action contrasts with the nearly horizontal or oblique position of the natatory trunk limbs or lateral lobes of epi-benthic animals. In benthic species, in which the endopods of post-oral head and trunk limbs were mainly ambulatory and vertical in position, the pre-oral appendages were essentially co-planar. In "*Laggania*"-like animals (Table I - *A. nathorsti* group), with 11-segmented limbs, the posterior marginal spines were exceptionally long and strong, as if utilized in raking or digging in soft sediments (Fig. 3D).

If the plane of action is rotated to the horizontal, the paired limb spines come into opposition as a prey-capturing and killing mechanism. In this manner, and through prolongation of the head region into a long flexible annulated proboscis, the terminal raptorial claw of the free-swimming *Opabinia* can be derived (Fig. 3B; Bousfield & Collins, in preparation). The paired spines on each side are 14 in number, as in *Anomalocaris canadensis*. The distal five of these are longer and more steeply oblique and probably served in prey capture, whereas the proximal nine pairs are stouter, shorter, and more perpendicular and may have served in holding, crushing, and possibly preliminary mastication. The form and function of the claw is analogous to a modern pair of pliers. However, it was probably activated by a combination of muscular and hydrodynamic processes. The transfer of food material rearwards to the mouth by the proboscis was probably similar to the action of an elephant's flexible trunk. The proboscis does not contain the anterior gut, as proposed by Sharov (1966) (per Callahan, 1979).

In a much more highly modified Upper Carboniferous, internally segmented, squidlike counterpart, *Tullimonstrum gregarium*, described in detail by Johnson & Richardson, 1969 (Fig. 7C.2), the terminal claw was more slender, and the spines, 13-14 in number on each side, were minute (Fig. 3C). Prey items were probably small and soft-bodied, possibly free-swimming plankters, or worms or insect larvae extracted from tubes in soft bottom sediments.

In a Lower Cambrian benthic species, *Cassubia infracambriensis* (Lendzion, 1975), the number of pre-oral limb segments was reduced to 7, and segments 2-5 had large medial spinose processes (Fig. 3E). Regrettably, the plane of motion is not precisely determinable from the single incomplete fossil specimen.

In a direction presumably leading to the chelicerates, the pre-oral appendage of the protochelicerates *Jianfengia* and *Yohoia* was reduced to 3-4 segments, the outermost being double-spined and movably pincering upon the inner marginal spine of segment 2 (Fig. 3F). Limb orientation was in a vertical plane and the movable distal spine had been

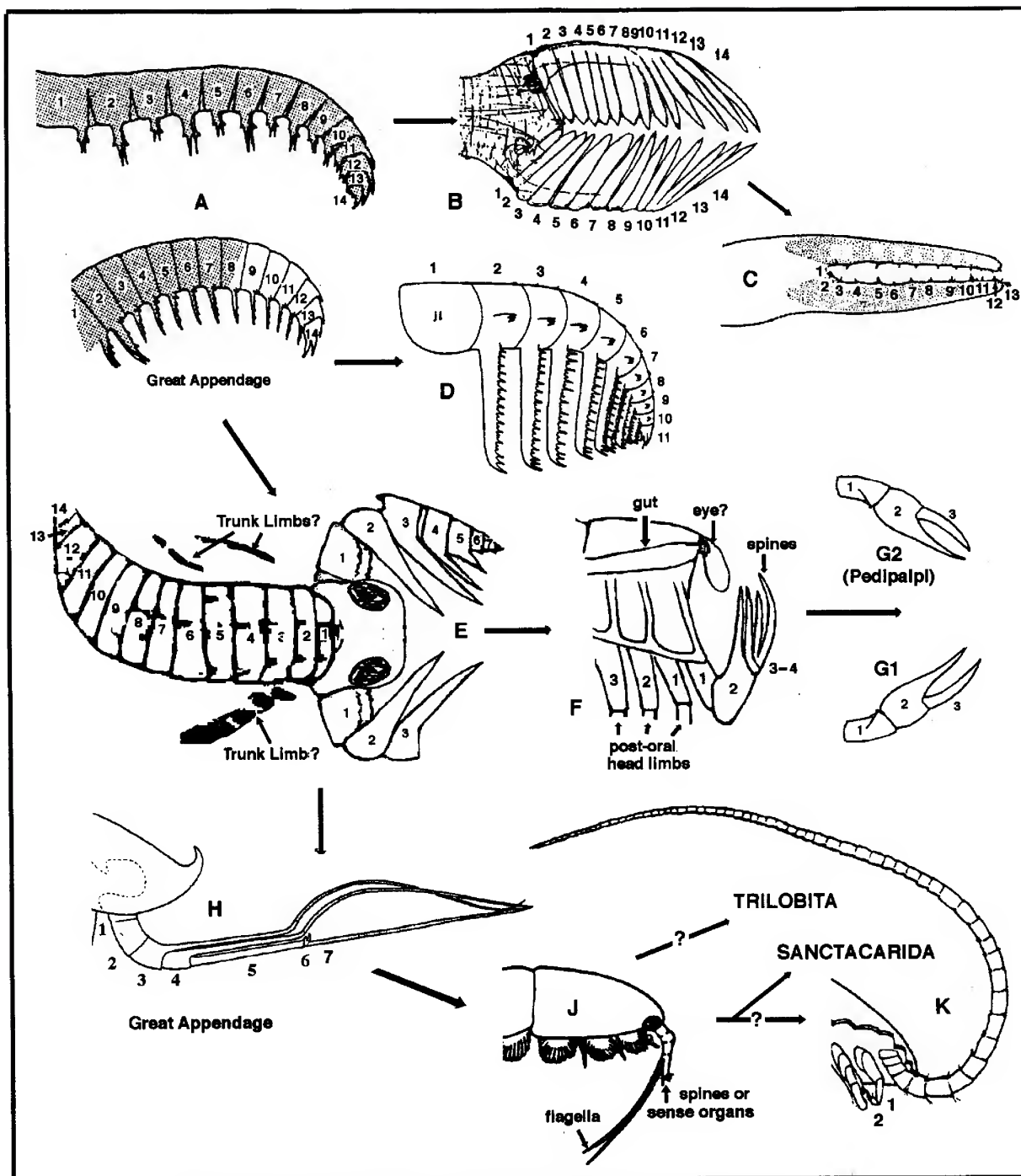


FIG. 3. PLAUSIBLE EVOLUTIONARY SCENARIOS IN THE PRE-ORAL APPENDAGE OF UNIANTENNATE ARTHROPODS (from Gould (1989) and various sources)

A. D. *Anomalocaris* spp. (Hypothetical Ancestral type)

Raptorial proboscoid line B. *Opabinia* C. *Tullimonstrum* (Carboniferous)

Raptorial chelicerate line E. *Cassubia* F. *Yohoia tenuis* G1. *Limulus* (late Palaeozoic)

Sensory flagellar line H. *Leancoilia* J. *Actaeus* K. *Emeraldella*

rotated to the lower or inner side, as in limuloids and phalangiate arachnids (Fig. 3G1). In eurypterids, scorpions, and pedipalpe arachnids (including spiders), however, the moveable segment is on the upper or outer side of the limb (Fig. 3G2). A major link in the presumed lineage from *Yohoia* to merostomatid arachnids is not confirmed from the fossil

record, viz., a yohoiid-like pre-oral appendage on a broadened head of 5 post-oral segments.

A further evolutionary thrust of the pre-oral uniantennate limb resulted in a filamentous sensory flagellum, represented in early stages by the form of the 7-segmented "great appendage" of *Leancoilia* (Fig. 3H). The inner marginal

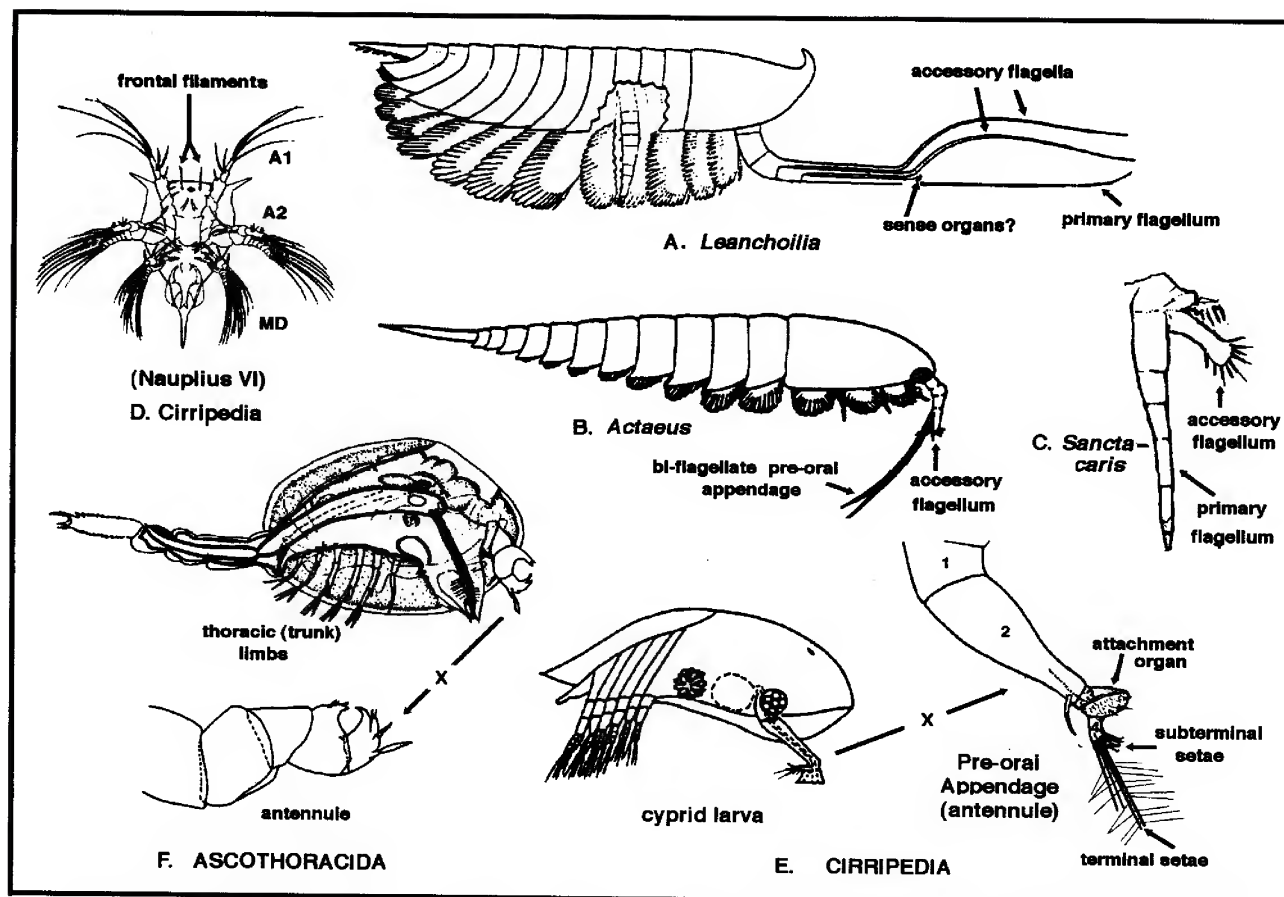


FIG. 4. PROPOSED HOMOLOGIES BETWEEN PRE-ORAL APPENDAGES OF MIDDLE CAMBRIAN TRILOBITOMORPH UNIANTENNATES AND ANTENNULES OF CRUSTACEAN (CIRRIPEDE AND ASCOTHORACID) BIANTENNATE ARTHROPODS (A,B,C after Gould, 1989; D, E, F after Schram, 1986)

spines of segments 3-4 and the terminal spine of segment 7 were apparently modified as a multi-segmented whip-like flagellum, whereas those of segments 5 and 6 were reduced to short stubs. In *Actaeus* (Fig. 7E.3), segments 3 and 4 remained flagellated, but 5-7 were much shortened, and bore short spine-like processes. In *Sanctacaris*, segment 3 (?) was short-flagellate and (?) 5-7 terminated in a star-like cluster of spines (Fig. 4C; 6D). Derivation of a 3-segmented chelicera from such an appendage would seem improbable. The simple elongate flagellar state is attained in *Alalcomeneus* (Fig. 7E.4), *Emeraldella* (Fig. 3K) and in most other trilobitoids, including the Burgessiiida and the Trilobita (Fig. 5E, F).

This analysis concludes that, in some evolutionary lines within uniantennate arthropods, the pre-oral appendage was initially a raptorial food gathering apparatus that secondarily became flagelliform. These morphotypes, including the trilobites, did not persist beyond the Paleozoic Era. In the evolution of primitive merostomes (e.g. *Chasmatspis*), a filiform antenna is unlikely to have disappeared, and a cheliform appendage suddenly appeared, as Bergström (1979) proposed for early chelicerates. The pre-oral appendage was already semi-cheliform in the proposed ancestral *Yohoia*. The trend from raptorial to sensory flagellar condition within the Trilobitoidea, rather than the reverse, is accompanied by

parallel evolutionary trends in cephalization of the head, gnathobasic development of ambulatory limbs, rearward shift of respiratory limbs, and in other major character states within component major sub-taxa (p. 22).

Within biantennate arthropods, however, the evolutionary picture is different. As revealed by the limited early fossil record, and the ontogeny of larval stages of extant and fossil forms, the pre-oral appendage appears to be filiform throughout, with few exceptions, as noted on page 14). The flagellate form has also persisted, with little change, in the myriapod and hexapod taxa that have dominated terrestrial environments since the close of the Paleozoic Era (Delle Cave & Simonetta, 1991).

Possible Homologies in Pre-oral Appendages of Uniantennate and Biantennate Arthropods.

As noted above, the significance of the first pre-oral appendage as a mechanism of food detection, food gathering, and general feeding style is basic in the Arthropoda. Both the organelles of the acron (e. g., frontal filaments, naupliar eyes) and the pre-oral first segmented head appendage are presumed sensors of environmental conditions and food sources. In uniantennates, the primary role of the latter was food gathering, a raptorial function that was retained in the

single successful line of uniantennate evolution, the Chelicerata. In the biantennates, however, the appendage was primarily sensory, at an early stage, and remained so throughout evolutionary history of all major subgroups. A comparison of pre-oral limbs of selected primitive morphotypes of both uni- and bi-antennates is pertinent (Fig. 4).

In the primitive trilobitomorphs, the pre-oral appendage passes through several stages of reduction of accessory flagella and sensory organelles (Figs. 4A, B, C), leading to the simple elongate flagellar condition of the Trilobita and Emeraldellida. In a few primitive maxillopodan crustaceans with specialized life styles, however, the appendages developed correspondingly specialized sensory and raptorial functions. In cirripedes, the antennules are natatory in naupliar and metanaupliar larvae (Fig. 4D), but become organs of site selection and attachment in the cyprid larvae of sessile, shell-burrowing and parasitic forms, the Thoracica, Acrothoracica, and Rhizocephalia respectively (Glenner & Hoeg, 1995) (Fig. 4E). These 4-segmented antennules bear a perhaps superficial but remarkable similarity, and almost certainly homologous relationship to, the pre-oral appendage of the primitive trilobitoid uniantennates, *Actaeus* (Fig. 4B), and *Sanctacaris* (Fig. 4C).

However, in the ascothoracidan biantennates, parasitic on echinoderm and anthozoan coelenterates, the antennule is raptorial in the cyprid and adult stages (Fig. 4F). The terminal two segments of the 4-segmented appendage, reminiscent of *Yohioia* (Fig. 3F), form a subchela for attachment to the host, or removal of pieces of the host tissue as food.

Perhaps a more precise concept of the pre-oral appendages of long extinct uniantennates of the Cambrian Period might be derived through closer study of the antennules of these very primitive extant crustacean biantennates.

The Pre-oral Appendage of Trilobitoid Uniantennates.

The general external morphology of selected trilobitomorph uniantennates is shown in Fig. 5. In *Burgessia* (Fig. 5A), *Molaria* (Fig. 5B) and *Habelia* (Fig. 5C), the head comprises four segments (five somites) which, in *Burgessia*, subtends a broad carapace covering the trunk segments. The post-oral appendages are ambulatory, those of the trunk also respiratory. The trunk terminates in a spikelike telson, similar to that of the merostomatid chelicerates, and suggests a strongly benthic life style. In *Sidneyia* (Fig. 5D), the head is only 2-segmented, but the anterior four trunk segments bear uniramous, powerfully gnathobasic limbs that are effectively part of the cephalic masticatory complex. The posterior 3 trunk segments are free and bear a broad, flabellate telson, evidence that *Sidneyia* was a powerfully swimming benthic and epibenthic predator.

In the trilobites, [e.g., *Naraoia*, a "soft trilobite" (Fig.

5E), and *Olenoides*, a primitive true trilobite (Fig. 5F)], the head is also 4-segmented, with 3 pairs of post-oral ambulatory, respiratory, and masticatory head limbs, and 11+ pairs of similar trunk limbs. However, trilobites differ from Burgessella in having a broad depressed head shield and trunk, the latter ending in a short pygidium or tail region of a variable number of segments. Both groups represent middle stages in cephalization of anterior trunk limbs.

Sanctacaris

On the basis of five well-preserved specimens from the Stephen Formation, near to but slightly younger than the Burgess Shale quarry, Briggs and Collins (1988) described a large carnivorous arthropod, *Sanctacaris uncata*, that they assigned to subphylum Chelicerata (Fig. 6). The broad head bears large eyes and six pairs of biramous appendages, the first five of which form a raptorial array of segmented, spinose and gnathobasic endopods with simple short antennalike exopods. The outer ramus of the sixth limb is also filamentous, but the inner ramus is short, terminating in a fringe of starlike radiating spines. The mouth is located anteriorly, presumably in a narrow gap between the first limb bases. The broad trunk is 11-segmented, the posterior bearing a paddle-shaped telson, the anterior 10 each bearing paired biramous limbs of which the exopod is large, flabellate, and natatory-respiratory in function. The inner ramus is slender, multi-segmented, and presumably ambulatory; marginal spines and/or gnathobases were not demonstrable.

However, another interpretation is utilized here. The biramous "sixth" appendage (Fig. 6D), bears a striking resemblance to the "transitional" pre-oral limb of *Actaeus*, with its star-shaped accessory flagellum (Fig. 5B), but unlike the raptorial condition in *Yohioia* (Fig. 3F; 7D) or the chelicerate condition in arachnids (Fig. 6F). Furthermore it arises near the eye, in a typically pre-oral position. The five pairs of raptorial head limbs of *Sanctacaris* have apparently been displaced forward beneath the head to form a raptorial "basket", immediately beneath the mouth. These limbs, although non-ambulatory, appear to be homologous with the five pairs of post-oral head limbs of *Emeraldella* (Fig. 6E). The latter has a single filamentous pre-oral flagellum that is apparently homologous with the short biramous "antenna" of *Sanctacaris*. In *Emeraldella* also, the post-oral head limbs are similar to the trunk limbs in being strongly ambulatory as well as gnathobasic.

On this interpretation, and in agreement with Delle Cave & Simonetta (1991), *Sanctacaris* is removed from the Chelicerata and placed in Class Emeraldellacea within the revised superclass Trilobitoidea (Table III, p. 24). *Sanctacaris* thus stands as a unique, relatively advanced, but apparently short-lived, sideline of Cambrian uniantennate evolution.

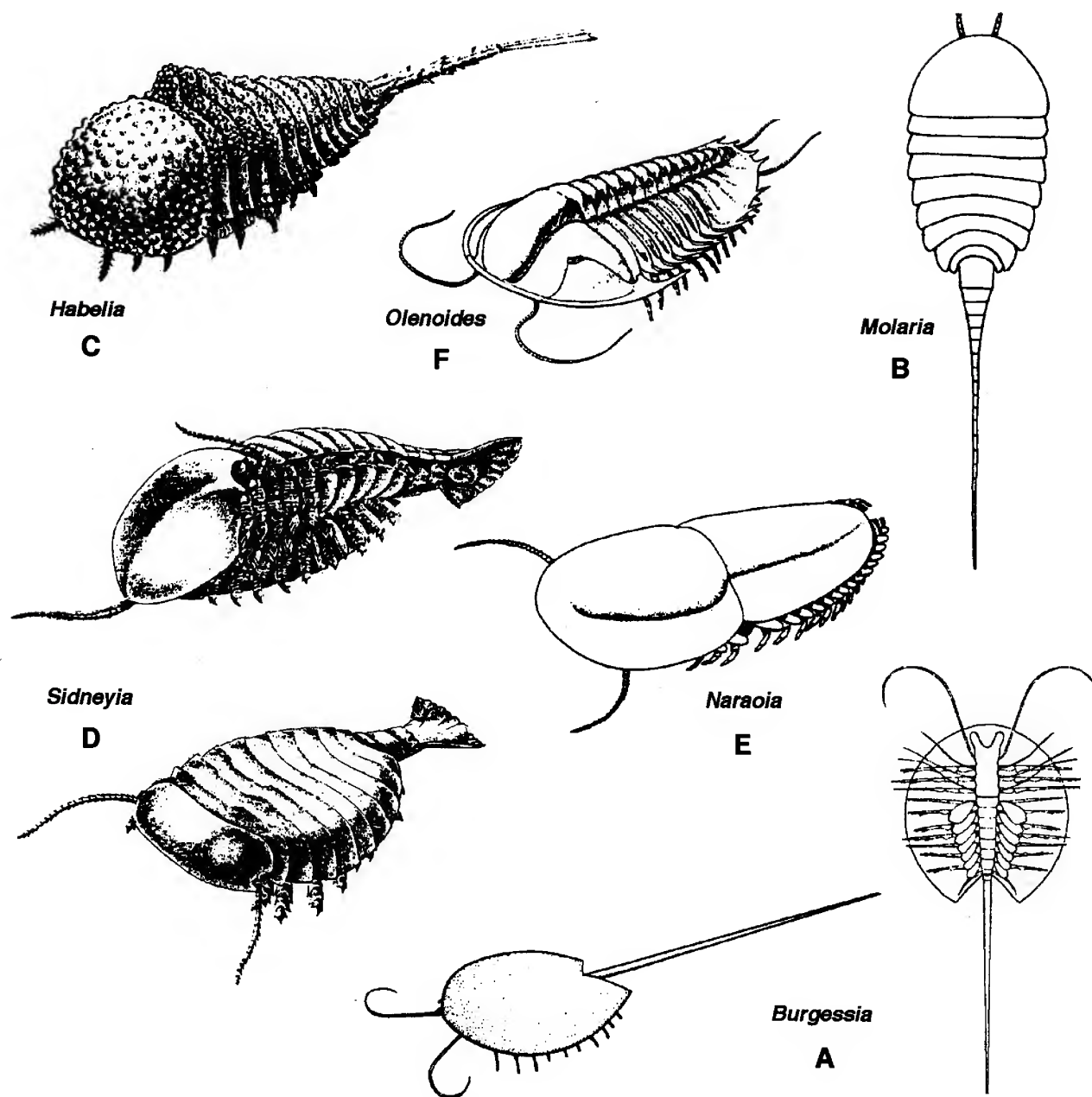


FIG. 5. CAMBRIAN ARTHROPODS: WITH GNATHOBASIC LIMBS AND FILAMENTOUS PRE-ORAL APPENDAGES (variously from Gould (1989) and Briggs et al (1993))

Evolutionary Pathways in Uniantennate Arthropods

Plausible evolutionary pathways within uniantennate arthropods of the Cambrian period that led to more highly evolved trilobitoid and chelicerate faunas of the middle and late Paleozoic are summarized in Fig. 7 (p. 17). The chart embodies information provided in Table I, and figures 2, 3, 5 & 6 especially. The degree of morphological evolution and specialization of feeding style is represented by four blocks or zones, proceeding along the X-axis, from the most primitive (pharyngeal feeding) on the left, through a narrow transitional band in the middle, to limb gnathobasic and limb

masticatory feeding types on the right. Of these, the chelicerate form on the extreme upper right is the most advanced. The Y-axis represents a generalized, rather than definitive, time scale.

As noted previously, the most primitive and presumably ancestral uniantennate arthropod of the late Precambrian, Vendian, and Early Cambrian Periods was a member of the predatory and pharyngeal-feeding Anomalocarida, illustrated on the lower left. These large-eyed animals possessed a short head (2-4 somites), and a multisegmented body with bilobate lateral pleurae or biramous ambulatory and respiratory paired appendages. In a cephalopodlike feeding

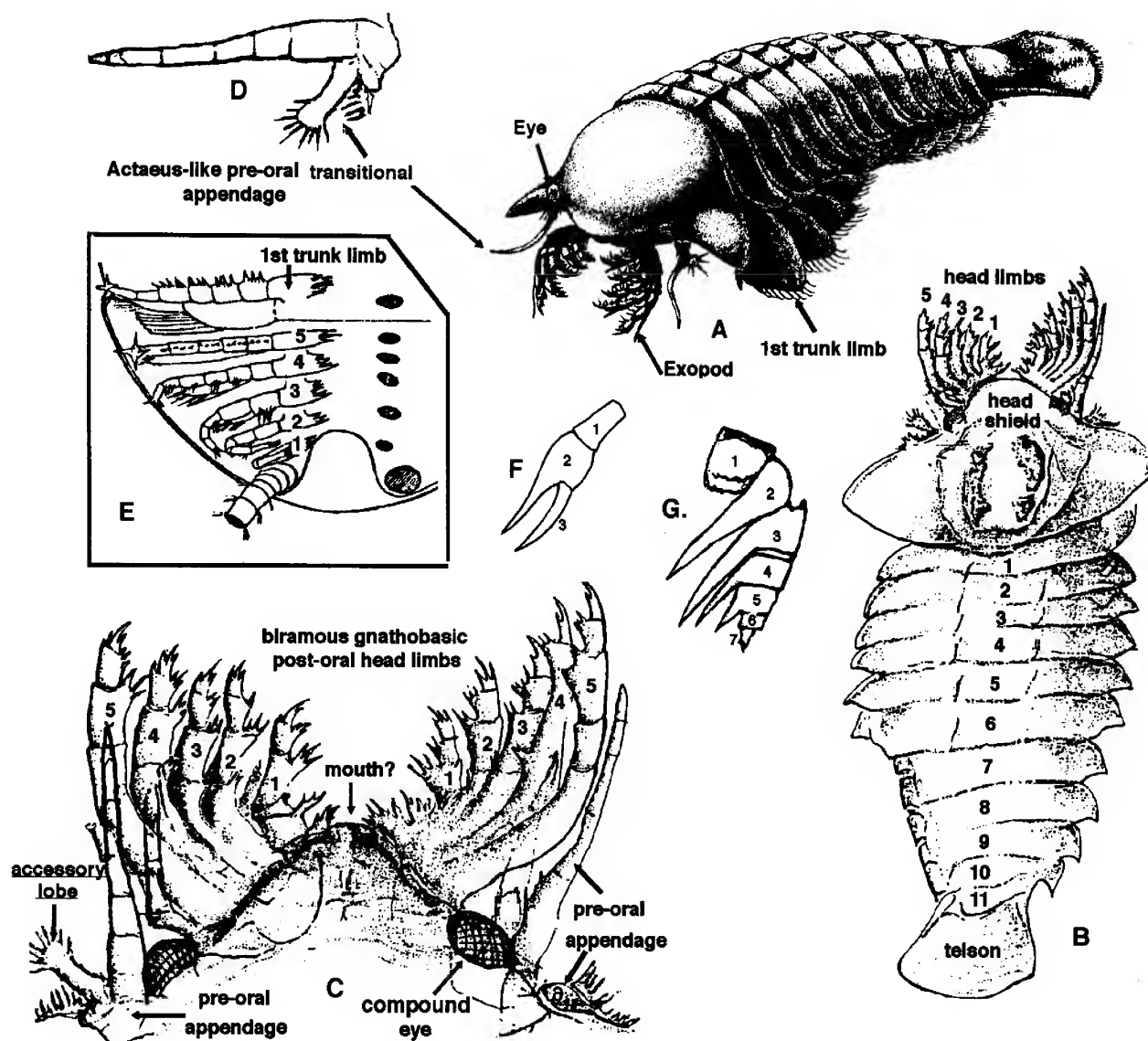


FIG. 6. EXTERNAL MORPHOLOGY OF *SANCTACARIS* (modified from Briggs & Collins, 1988)
A. Life-like Reconstruction. B. Dorsal View. C. Head region (MAG. X), D. Pre-oral appendage (X)
E. (Inset). Head appendages of *Emeraldella* (ventral view)
F. *Limulus* Left chelicera G. *Cassubia* Left Pre-oral Appendage.

style, paired raptorial pre-oral head appendages apparently captured and transported food to the mouth region where it was masticated and ingested without post-oral limb assistance. Within the Anomalocarida *per se*, development of a benthic life style was accompanied by reduced segmentation but stronger armature, possibly partly fossorial in function, of the pre-oral raptorial limbs (e.g., in "*Laggania*" - type fossils (Table I) and in *Cassubia* Lenzion, 1977, centre line).

Of the three proposed evolutionary offshoots from the Anomalocarida, the epibenthic probosciferidans (on the left) developed a very specialized food capturing mechanism, similar in function to the heterocotyl arms of cephalopods, but found nowhere else among the arthropods. It consisted of horizontally opposing limbs fused together in a claw-like

appendage that was activated by a flexible proboscoid extension of the anterior head region. Its movements were presumably triangulated and co-ordinated by widely set pairs of stalked compound eyes. The small size of this "proboscis", and lack of peribuccal or pharyngeal teeth, indicate that the prey organisms were very probably small and soft-bodied.

Cladistic presentation of relationships of *Tullimonstrum* by Beall (1991) may be a case of "bending the facts" to fit theoretical models. None of his cladograms provides close relationships between *Tullimonstrum* and other major invertebrate groups, and each cladogram contradicts relationships depicted by the others. The "re-interpreted" animal appears unfunctional (e.g., a vertical tail on a depressed trunk) and inconsistent with the taxonomic details of Richardson (1966) and Johnson & Richardson (1969) that resulted

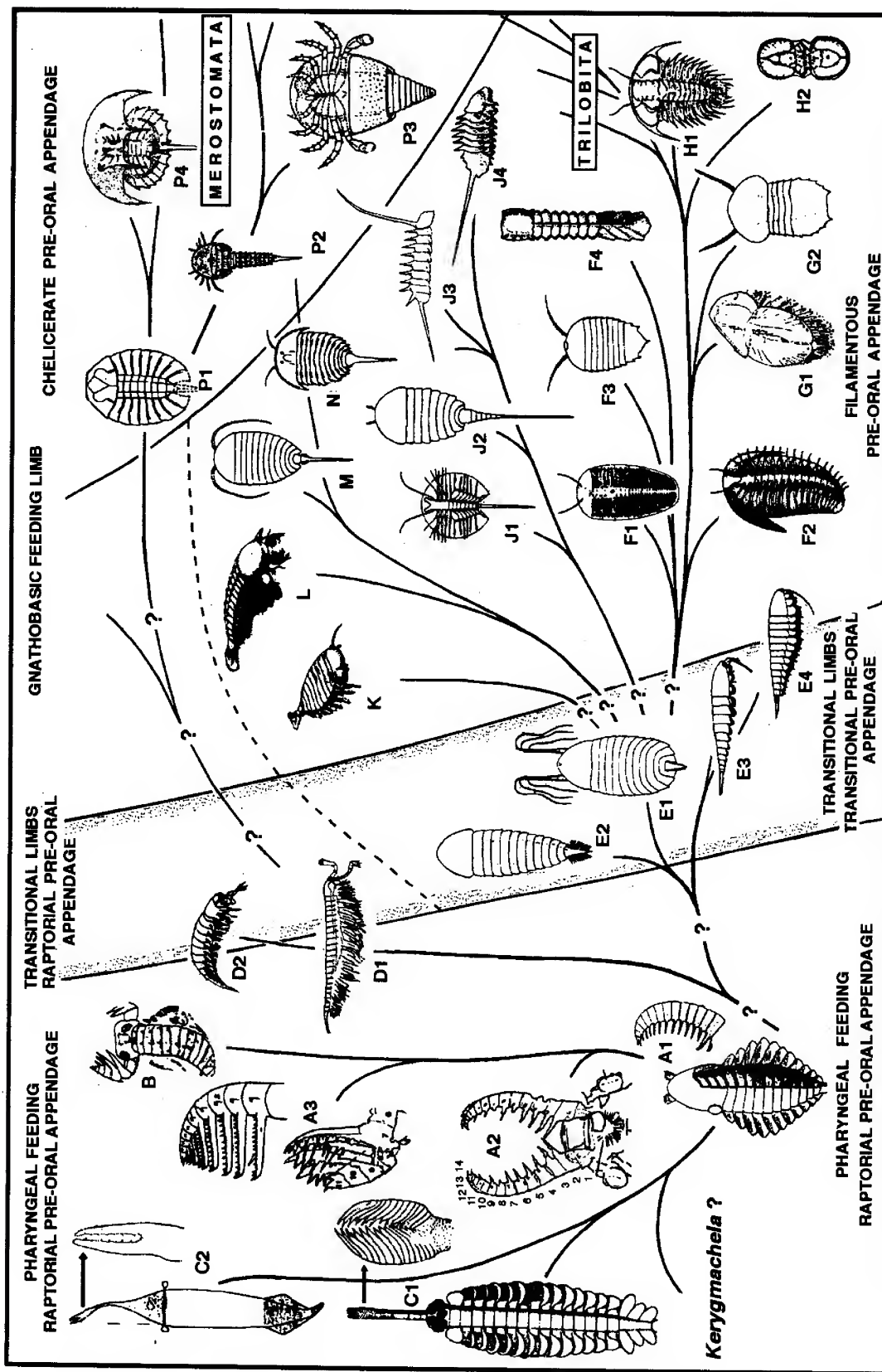


FIG. 7. RELATIONSHIPS OF CAMBRIAN UNIANTENNATE ATHROPODS BASED ON FEEDING MECHANISMS

FIG. 7. RELATIONSHIPS OF CAMBRIAN UNIANTENNATE ATHROPODS BASED ON FEEDING MECHANISMS

A1. *Anomalocaris canadensis* A2. *Anomalocaris* sp. (Chengjiang) A3. *Anomalocaris nathorsti* B. *Cassubia*
 C1. *Opabinia* C2. *Tullimonstrum* D1. *Jianfengia* D2. *Yohoia* E1. *Leanaoilia* E2. *Acanthomerion* E3.
 Actaeus E4. *Alalcomenaeus* F1. *Nathorstia* F2. *Tegopelte* F3. *Kumaia* F4. *Mollisonia* G1. *Naraoia* G2.
 Liwia H1. *Olenoides* H2. *Agnostus* J1. *Burgessia* J2. *Molaria* J3. *Economocaris* J4. *Thelxiope* K. *Sidneyia*
 L. *Sanctacaris* M. *Emeraldella* N. *Agataspis* P1. *Triopius** P2. *Chasmatspis* P3. *Diploaspis** P4. *Euproops*†

*L. Ordovician †Devonian ‡Carboniferous

from careful observations on numerous specimens.

A more successful evolutionary experiment typifies the mostly benthic trilobitoid line to the right. In it, the pre-oral limb lost its raptorial function and became flagelliform, multi-segmented, and presumably mainly sensory and perhaps tactile in function. Simultaneously, the post-oral head and trunk limbs developed a linear gnathobasic endopod which, through various degrees of cephalization of anterior trunk segments, formed a masticatory feeding field of 2-5 pairs of post-oral head appendages. Remarkably, the species of *Leancoiliidea* (including *Acanthomeridion* from Chengjiang deposits) sit squarely in the transitional zone of both pre- and post-oral limb evolution. *Alalcomenaeus*, having the most advanced, mono-filamentous pre-oral appendage, also has nearly fully gnathobasic post-oral appendages (Delle Cave & Simonetta, 1991).

Of the flagellated trilobitoids with 3 post-oral head segments, the "spike-telsonic" group (centre right) encompassed the *Habelia* subgroup having armoured processiferous bodies and short antenna. The associated *Molaria*, also having filamentous antenna and only three post-oral head segments, is an unlikely precursor of the chelicerates, as proposed by Delle Cave and Simonetta (1991, Chart II). Trilobitoideans with pygidial (non telsonic) abdomens (lower right) included narrow-bodied "idotheid" or "asellid" isopod-like forms such as *Mollisonia* and *Urokodia* that may have occupied algal substrates. They also included broad, flat-bodied, fossorial types with protective exoskeletal armour, leading to their only successful subgroup, the trilobites, that diversified in the later Paleozoic times.

The trilobitoids include the Emeraldellidacea that have 5 post-oral head segments and a spike-like telson (upper right). The group here includes the aglaspidids, thought to possess chelicerae prior to the work of Briggs et al (1978). Aglaspidids "straddle" the Upper Cambrian-Lower Ordovician boundary. The Devonian *Cheloniellon* may be a distant descendent of the main line of Emeraldellidae. As mentioned above, a carnivorous form with paddle-like telson, *Sanctacaris*, is considered an early offshoot of this same line. This species has 5 distinct post-oral head segments, each with biramous paired raptorial limbs. *Sidneyia* has no post-oral head limbs but the first four trunk limbs are uniramous (lacking gills), strongly gnathobasic and form, effectively, a post-oral masticatory field of four segments. *Sidneyia* is here regarded as a very early (relict) stage of cephalization of anterior trunk appendages, and had a separate origin (Fig. 7K).

The most successful anomalocarid offshoot is here believed to be the *Jianfengia-Yohioia* line, to the upper right of Fig. 7. The post-oral head limbs, in the process of losing respiratory exopods, were already ambulatory and transitional in form. Although the pre-oral head limbs remained raptorial, their reduced size and segmentation and subcheliform appearance are plausible precursors to the fully chelicerate condition found in the most primitive arachnids, the merostomes, of the Lower Ordovician (upper right). However, the viability of this proposed evolutionary connection awaits discovery of a broadly flat-bodied fossil having transitional

masticatory post-oral head and trunk limbs and a more clearly cheliform (rather than geniculate) pre-oral appendage. *Triopus* (Fig. 7P.1) may approach that predicted form but its appendages are poorly known. *Chasmataspis* (Fig. 7P2) is the most primitive Lower Ordovician undoubted chelicerate, leading to the eurypterids. Although not completely understood (Bergström, 1979), *Chasmataspis* has 5 post-oral head segments and 12 trunk segments. The total is one more than the combined number of post-oral segments of the presumed ancestral *Yohioia*.

The Euthycarcinoidea Enigma

The enigmatic group of aquatic arthropods classified as Euthycarcinoidea, is based on a half-dozen limnic (?) species that existed from Carboniferous to Triassic time. Bergström (1979) summarized information on the Triassic genera *Euthycarcinus* and *Synaustrus*, and Schram and Emerson (1991) utilized the upper Carboniferous genera *Pieckoxerxes* and *Kottixerxes* in developing their newly proposed Arthropod Pattern Theory (Fig. 8). The broad head shield is typically composed of 3 somites including an eye-bearing acron, an anterior procephalon with a single pair of filamentous antennae, and a posterior gnathocephalon bearing a set of mandible-like appendages and on which the mouth opens ventrally. The broadened trunk is divided into an anterior (thoracic) region of diplo- or triplo- segments each bearing paired uniramous limbs, and a posterior narrower and limbless abdomen that terminates in a spikelike telson.

According to Schram & Emerson (loc. cit.), the possession of uniramous limbs and diplosegments may link these animals to the ancestry of the terrestrial myriapods and hexapods (Uniramia of Manton, 1972). On the other hand, the overall appearance of euthycarcinoideans is grossly similar to some uniantennate arthropods having 3-6 head segments, and filamentous pre-oral limbs, e.g., *Leancoilia*, *Habelia*, and *Emeraldella*. However, unlike the uniantennates, the trunk endopods are filamentous, multisegmented, and lack raptorial spines, gnathobases, and/or terminal claws. The leg segments bear slender posterior marginal spines that are possibly of both natatory and respiratory support function, and in that respect resemble the exopods of some uniantennate arthropods (e.g., of Trilobitoidea).

The Lower Cambrian Chengjiang fossil deposits in Yunnan region, South China, discovered in 1984, contain a number of very primitive arthropods yet imperfectly known, and mostly not included here. However, one of these, *Fuxianhuia protensa* Hou, 1987b, is remarkably similar in overall form to the euthycarcinoideans (above, and figs. 8A, 9) as detailed recently by Chen et al. (1995) (Fig. 8 A-H). The body consists of a short, broad, head shield and an elongate trunk region. The latter is divided into a thorax of 17 broad, depressed, limb-bearing segments, and an abdomen of 14 narrower and more cylindrical, legless segments, the last bearing a prominent telson spine. The head bears an anterior pair of large stalked eyes, a pair of filamentous pre-oral appendages (antennules) on somite 2 and, ventrally on

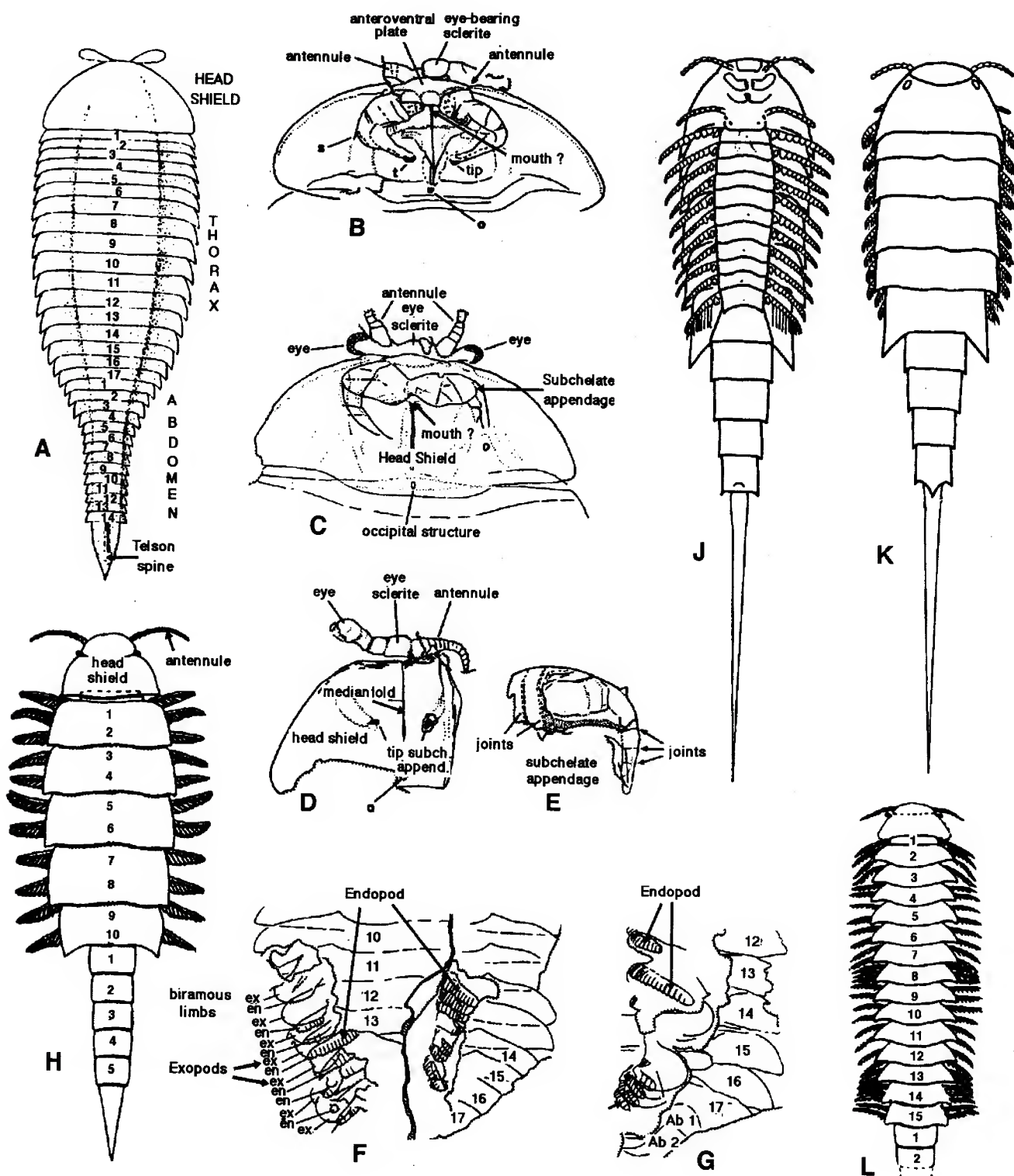


FIG. 8. EUTHYCARCINOIDEA: *Fuxianhuia protensa* Hou, 1987 (Middle Cambrian)
A. Dorsal reconstruction Head shield **B., C.** ventral reconstr. **D.** dorsal reconstr.
E. Subchelate head appendage **F.** Abdomen, ventral **G.** Abdomen (ventral X. 1987;
 showing limbs) **H.** *Pieckoxerxes piekoe* **K.** *Kottixerxes gloriosus* (A, B - after Hou,
 D-G (after Chen et al, 1995) H, L. (after Schram & Emerson, 1991).
 J, K, *Euthycarcinus kessleri* (after Bergström, 1979).

somite 3, a pair of subchelate raptorial limbs, presumably arising on either side of the mouth. These superficially resemble the raptorial head limbs of the uniantennate arthropod *Cheloniellon*, the raptorial maxillae of remipede crustaceans, and the raptorial first thoracic limbs of belostomatid hemipteran insects. However, they are unlike the paired palpless mandiblelike structure of the mouth region ascribed to a few specimens of *Euthycarcinus* (Bergström, 1979).

In other details, however, the similarity of *Fuxianhuia* to euthycarcinoideans is remarkably close. The trunk limbs are biramous, with thin plate-like exopods, but the endopods are cylindrical, multisegmented, and lack terminal claws. These endopods are also similar to the multisegmented, basally shafted rami of larval skaracarids of the Cambrian "Orsten" fauna (Fig. 9, part). The limbless abdomen is found elsewhere in most maxillopodan crustaceans (e.g., several Skaracarida, Cirripedia, Copepoda, etc., and the Cephalocarida) as well as some phyllocaridans and phyllopod biantennates. The incomplete basal fusion of the trunk exopods and endopods is reminiscent of the lateral lobe-like paired flaps or limbs of the primitive dicephalosomatid uniantennates. Modern aquatic predators with "jackknife" raptorial limbs (above) are all free-swimming pelagic predators, perhaps indicating a similar life style in euthycarcinids.

In summary, *Fuxianhuia* bears some similarity to nearly every major group of arthropods of the Lower and Middle Cambrian Period but does not conform completely with any. In the very primitive structure of his head and locomotory limbs, and multi-segmented body, it is close to a model arthropod ancestral type (e.g., of Snodgrass, 1956). However, the presence of two pairs of pre-oral head limbs, the first of which is filamentous and the second raptorial, is similar to the situation in crustaceans and some phyllocaridans, and thus essentially biantennate. This feature, along with the multisegmented, clawless endopods of the thoracic region, justify its inclusion within the class Euthycarcinoidea. Its other members are of more recent geological age, but sufficiently distinct to justify erection of the primitive subclass Fuxianhuiacea (Table IV, p. 27).

Evolutionary Relationships in Aquatic Biantennates

A recapitulation of plausible evolutionary pathways within early aquatic biantennate arthropods is sketched in Fig. 9. On the left of the chart are connectives for two genera of skaracarid crustacean larval forms, a phosphotocopine ostracod, and a thecostracan cyprid, that represent the primitive evolutionary phases of skaracarid, ostracod and cirripedian maxillopodans of Cambrian times. Their primitive character states included the shaftlike form of the basal portion of the post-oral head limb endopods, the unbossed condition of their ramal spines and setae, and the multisegmented rami that are found variously in early naupliar stages of Copepoda, Cirripedia, and other extant maxillopodan crustacean subgroups. The systematics and evolutionary history of maxillopodan crustaceans are relatively well known (e.g., in Schram, 1986), and are not discussed further here.

In the centre are the euthycarcinoideans of which *Fuxianhuia* from the Lower Cambrian is here designated the most primitive member. The Upper Carboniferous and Triassic members are shorter-bodied, with diplo- and triplo-trunk segments, uniramous limbs, and may be ancestral to groups with the Myriapoda. However, further evidence from Silurian and Devonian representatives is needed to clarify such a phylogeny.

To the centre right are connectives between the three subclasses of biantennates recognized here within a revised and restricted definition of Latreille's original crustacean class Phyllopoda (p. 26). These Cambrian groups resemble extant branchiopodan and leptostracan crustaceans, at least superficially, and may have had a late Precambrian or Vendian common ancestor. The branchiocarids and odaraiaids were regarded as unique arthropods and/or crustaceans by Briggs (1976, 1981). However, they differ from true crustaceans in the 3-segmented head structure (lack of clearly defined maxillae and maxillary segments) and the carapace is mandibular rather than maxillary in origin. Although Schram (1986), following Briggs (1978), assigned the Canadaspida to Malacostracan subclass Phyllocarida, Dahl (1984, 1987) convincingly demonstrated primary differences of tagmatization, total number of body segments, position and form of the presumed mandible, limb structure and other anomalous features that, under existing definitions, remove the Canadaspida from the Phyllocarida, and the true Crustacea.

In Fig. 9, lower right, are the marrellomorphs. These represent one of the few aquatic biantennate arthropods with qualifications for direct ancestry to the myriapods and hexapods, its leg features postulated by Kukalova-Peck (1992). Thus, marrellomorphs are biantennate and the head limbs possibly mandibulate, but not ambulatory-gnathobasic. They are mainly benthic in life style and the anterior limbs are apparently double-clawed, suited to walking or crawling over firm substrates. They also possess similar body tagmatization and limb structure, and the telson is minute or lacking. The leglike maxillary and labial palps of *Dasyleptus*, an Upper Carboniferous monuran wingless insect (Fig. 9) are remarkably similar in form to the endopods of the ambulatory head limbs of the Devonian marrellomorphs *Mimetaster* and *Vachonisia* (Stürmer & Bergström, 1976). Loss of the second head segment and its antennalike pre-oral limbs in myriapods and hexapods accords with overall evolutionary trend to reduction of limbs and accessory lobes that accompany a shift from aquatic to terrestrial life style. In air, gravitational effects on limb structure are more significant; two pairs of sensory limbs would thus appear to be mechanically unwieldy and functionally unnecessary.

Phylogenetic Tree of the Arthropoda

An annotated classification of uniantennate and biantennate arthropods is presented in Tables III (p. 25) and IV (p. 27) respectively, the number of higher categories of which are summarized in Table V (p. 29). Hypothetical

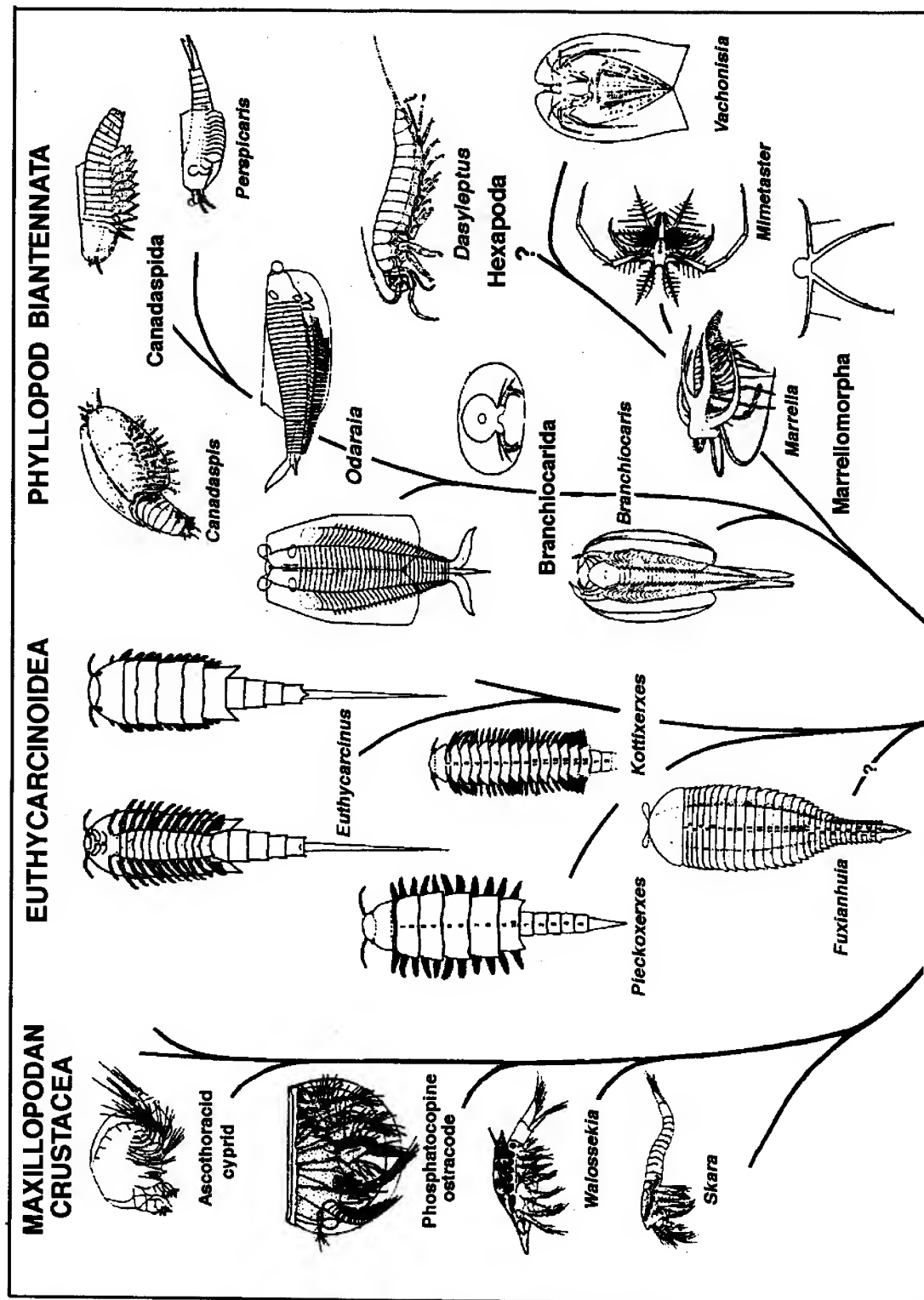


FIG. 9. PHYLETIC LINKAGES WITHIN BIANTENNATE ARTHROPODS OF THE PALEOZOIC ERA

FIG. 9. PHYLETIC LINKAGES WITHIN BIANTENNATE ARTHROPODS OF THE PALEOZOIC ERA

Maxillopoda - after Schram, 1986; Euthycarcinoidea - after Bergstrom, 1979; Schram & Emerson, 1991; Chen et al, 1995; Phyllopoda - after Gould, 1989; Marrellomorpha - after Bergstrom, 1979; Hexapoda - after Kukalova-Peck, 1987).

relationships of the major genera of the Cambrian Period to each other and to other major groups of arthropods over the 600+ million year geological and evolutionary time scale are summarized in the accompanying chart (Fig. 10, p. 23).

Phyletic relationships may be presented in a number of graphical ways, including cladograms (e.g. Briggs & Fortey

1989), following an earlier attempt by Briggs (1983). Those authors (1989) utilized 26 characters and corresponding character states in deriving an arrangement in which the biantennate branchiopods clustered near the base, the trilobites at the advanced end, and various trilobitoideans and arachnids at intermediate levels of the evolutionary

scale. Whereas this scheme has an overall plausibility, it is limited in detail by the omission of dicephalosomatid arthropods or other related outgroup taxon, by other possibilities in the ordering of some character states, and by weaknesses inherent in cladistic analyses generally (see Gosliner and Ghiseln, 1984).

In view of limitations of cladistic methodology at this stage of knowledge, the writer finds merit in modifications of the simple phyletic tree arrangements of Delle Cave & Simonetta (1991), for various early arthropod subgroups, as outlined here in Fig. 10. The hypothetical "tree" commences somewhere within late Precambrian times, in conformity with the views of Dzik & Krumbiegel (1989). Thus, representatives of tardigrade and onychophoran pararthropods and both uniantennate and biantennate arthropods were already present in the earliest (Lower Cambrian) fossil deposits (Dzik & Lendzion, 1988). Also, protarthropods (e.g. *Xenusia*) and some antennognath arthropods (e.g., *Spriggina*, *Praecambridium*) are also known from Ediacrian and Vendian fossil deposits (Delle Cave & Simonetta, 1991).

The earliest and morphologically most primitive uniantennulate subgroup of Cambrian times is here considered to be the dicephalosomatids (p. 25). The primitive anomalocarids did not survive the Cambrian and the more advanced probosciferans lasted only until the Upper Carboniferous. The Yohoiida, possibly on a direct ancestral line with the chelicerates, also became extinct in the Cambrian. Not yet discovered, however, is a theoretical Cambrian fossil form having a 6-segmented head, transitional post-oral masticatory limbs, and fully cheliceriform pre-oral appendages that might directly link the group with the chasmataspids and primitive aquatic arachnids of Ordovician and later periods. Of the aquatic merostomes, the eurypterids diversified during the mid Paleozoic but became extinct prior to the Mesozoic, and a few relict limulids are the only modern survivors of those primitive aquatic chelicerates.

The Trilobitoidea embodied various combinations of head and trunk segments having filiform, sensory pre-oral appendages and raptorial, gnathobasic, post-oral feeding and ambulatory limbs. Several of these, including early trilobites (e.g., olenellids) apparently became extinct during the Cambrian, although the Emeraldellidea persisted until the Devonian (e.g., *Chelionellon*). The more advanced trilobites became the single most speciose and diverse group of aquatic uniantennates during the early Paleozoic. They apparently survived longer than any other other arthropod group having only 4 head segments, but were gone by the beginning of the Mesozoic.

The paleohistory of the biantennates is less clear. Primitive biantennates, the euthycarcinoids, marrellomorphs and phyllopods occurred, even abundantly, in the Cambrian. However, the marrellomorphs survived only until the Upper Paleozoic, and the euthycarcinoids to the Triassic. As noted on page 18, the marrellomorphs provide a plausible (but not confirmed) aquatic ancestor to the terrestrial myriapods and hexapods whose fossil records commenced in the lower Devonian and upper Silurian periods. Kukalova-Peck (1992)

has provided convincing evidence that the myriapod and hexapods could not have originated from the Xenusian-onychophoran line of "uniramians", a conclusion supported by the present study.

The fossil record of early crustaceans is uneven, but little doubt exists, especially as result of remarkable new micro-fossils in the Swedish 'Orsten' deposits, revealed by Walossek & Müller (1989), that the maxillopodans were a very diverse biantennate group by Middle and Upper Cambrian times. Maxillopodans continued to exploit aquatic niches and food resources in which small size, free-swimming metamorphic developmental stages, and filter-feeding mechanisms are advantageous. The somewhat larger Branchiopoda, by developing a resting egg stage, have managed to survive, mainly in temporary freshwater habitats, over a comparable time frame. Their non-palpal mandible, even in early naupliar stages (Sanders, 1963), may indicate an early link with the Phyllopoda. There is little basis for a direct phyletic link with the trilobitoideans, as studied by Hessler & Newman (1975).

With respect to the Cephalocarida and the Remipedia, crustacean classes discovered only during the later half of this century, their body and limb structures are more primitive than most other maxillopodans, and certainly the malacostracans (Schram, 1986). Despite their problematical late Paleozoic (or non-existent) fossil records, an early Paleozoic origin for both groups is a reasonable expectation.

The Malacostraca may be considered the dominant and most diverse crustacean class of Recent times (Bousfield & Conlan, 1990). Transfer of the orders Canadaspida and Branchiocarida from the Crustacea to the phyllopod Biantennata (p. 25), leaves the Upper Devonian protoglyphaeid reptantian *Palaeopalaemon newberryi* as the earliest confirmed malacostracan fossil record (Schram, 1986). However, the relatively plesiomorphic body segmentation and limb structure of the Leptostraca (*sensu strictu*), as well as the Hoplocarida and Syncarida, would suggest a somewhat earlier beginning for the malacostracans, possibly during the Silurian or late Ordovician.

THE CAMBRIAN ARTHROPOD FAUNA: EVOLUTIONARY TRENDS.

Early trends in the direction of morphological and behavioural evolution in arthropods, revealed by Burgess Shale and other Cambrian faunal assemblages, are summarized as follows:

- (1) Within uniantennate arthropods, the ancestral pharyngeal and peribuccal feeding methodology was replaced by a masticatory assemblage of post-oral gnathobasic limbs of the head region. The taxonomic series of *Anomalocaris*, *Leanchoilia* and *Emeraldella* represents this transformational process.
- (2) Also within the uniantennates, the primitively large raptorial food-gathering limbs of the pre-oral head region gave rise to short, paired cheliform and chiefly masticatory appendages within the higher (terrestrial) Chelicerata. The



(Based partly on Schram (1986) and Bousfield & Conlan (1990))

taxonomic sequence of *Anomalocaris*, *Yohoia*, *Chasmatspis*, and the Scorpionida illustrates this evolutionary sequence.

(3) Other types of pre-oral limb development that involved an opposing limb raptorial mechanism on the one hand, and a filamentous sensory structure on the other, did not survive the close of the Paleozoic Era.

(4) The cephalization, or incorporation of masticatory limbs of anterior trunk segments into the head shield, of both uni- and bi-antennate arthropods, proceeded most rapidly during the Cambrian Period. Such a rapid evolutionary process in major taxonomic features may prove to be a direct example of punctuated equilibrium proposed by Eldridge & Gould (1972). However, few aquatic taxa with only 2-4 head somites (e.g., a few Probosciferida, Marrellomorpha) survived beyond the Cambrian, although the euthycarcinoids persisted until the Triassic; some with five somites (e.g., Trilobita) reached the late Paleozoic; whereas groups with 6-7 head somites (e.g. Crustacea, Chelicerata) extended into Mesozoic and Recent times.

(5) Primitively shaftlike and elongate trunk limbs became increasingly distinctly segmented, chitinized, and shortened, especially in benthic forms. A series of forms within the crustacean order Skaracarida (e.g. *Dala*, *Bredocaris*, and *Oleandocaris*), the phosphatocopine ostracods, and the naupliar-metanaupliar stages of other maxillopodan crustaceans, illustrate such transformation.

(6) The dorsal shield arises from the first head segment (pre-oral carapace) in primitive, pharyngeal-feeding arthropods. In more advanced, limb-masticatory arthropods (e.g., mandibulates) the carapace (secondarily bivalved) arises from the posterior segment of the head shield that is mandibular in phyllopods and typically maxillary in crustaceans.

(7) With respect to the natatory function of limbs, swimming appendages occur in both post-oral head and trunk regions of very early uniantennates, and larval stages of more advanced arthropods. Coincident with tagmatization of the trunk into thorax and abdomen, and the "cephalization" of feeding limbs in higher taxa, swimming, and respiratory, functions shifted posteriorly from head to thorax and finally to abdomen, as in stomatopods, isopods, and other Malacostraca.

(8) Evolution of the terrestrial myriapods and hexapods from presumed aquatic ancestors apparently involved loss of the second pre-oral head segment and its antennate appendages. In the aquatic environment, those limbs are functionally sensory (see Callahan, 1979), locomotory, or even food gathering. In the terrestrial environment, such limbs presumably became duplicative and mechanically unwieldy, and followed into oblivion the original prothoracic wings of insects. Similarly, in peracaridan crustaceans that have become secondarily terrestrial (e.g., talitrid amphipods, oniscoidean isopods), one of the sensory antennal pairs (first, antennules) has become very much reduced or vestigial, with only one pair (second, antennal) remaining effectively functional. In similar vein, an alternative functional evolution

of the head appendages of myriapods and hexapods would countenance the fusion of the first pre-oral limbs to the labrum to form the clypeo-labrum, and the second pair of head appendages, equivalent to the second antennae of crustaceans, have become the monofilamentous antennae of the hexapods. However, embryological and/or paleohistorical (fossil) evidence for such a proposal has not yet been demonstrated.

In summary, in the most successful arthropod groups of modern times, the head shield encompasses anterior limbs of the primordial trunk region, limbs that assist in food capture and mastication. Body tagmatization has become pronounced, and swimming, ambulatory and respiratory functions are relegated increasingly to thoracic and abdominal limbs (see also Schram, 1986). In higher crustaceans (malacostracans), thoracic limbs have become uniramous, cheliform and versatile, and the antennules secondarily bi- or tri-ramous and sensory. In higher arachnids, however (e.g., pedipalps and phalangids), the prosomal limb gnathobases have become secondarily lost, but feeding mechanisms remain primitive in the retention of chelicerate pre-oral limbs and a suctorial pharynx. In tracheates, the exopods of trunk limbs have been lost. In hexapods, the abdominal limbs have become vestigial or lost entirely, and exites of limbs have secondarily become gills and/or tracheae in the abdomen, and tracheae and/or wings in the thorax (see Kukalova-Peck, 1987, 1992). Such fundamental morphological changes in arthropod body form have unquestionably contributed vitally to the ability of modern groups to utilize the diverse organic and plant-related food resources that have evolved mainly in terrestrial habitats, and mainly since the late Paleozoic Era.

Source references for taxonomic and classificatory names and time-scale occurrences in following Tables III-V are: E. L. Smith - unpublished MS "Atlas of Insect Morphology"; L. Størmer (1959) - in *Treatise on Invertebrate Paleontology*; J Bergström (1979) - "Morphology of Fossil Arthropods"; S. J. Gould (1989) - "Wonderful Life" & source materials; D.E.G. Briggs et al. (1993) - "The Burgess Shale fauna" and source material; L. Delle Cave & A. M. Simonetta (1991) - "Early Palaeozoic Arthropods"; T. Savory (1964) - "Arachnids"; F. R. Schram (1986) - "Crustacea"; and numerous other source papers including arthropod sections in "Synopsis and Classification of Living organisms", McGraw Hill, 1982.

A database for analysis of the paleohistorical occurrence of major taxonomic groups is given in Table V (p. 28). Some taxonomic names, especially those relatively recently published or not sufficiently well described (e.g., *Waptia* Walcott, 1912) have been omitted from the lists and the analysis. A complete bibliography of citations of taxonomic names is not included in the references here, but may be found in the Zoological Record or other basic reference texts for the taxa, author names and dates concerned.

TABLE III. SUGGESTED NATURAL CLASSIFICATION OF AQUATIC, ESPECIALLY EARLY PALEOZOIC, ARTHROPODA BASED ON FOOD-GATHERING AND FEEDING MECHANISMS.

PHYLUM ARTHROPODA

I. INFRAPHYLUM UNIAENTENNATA, new name (= **MANDIBULOPODA** E. L. Smith "Atlas")

One pair of positionally and embryonically pre-oral head limbs; trunk limbs often gnathobasic.

†**SUPERCLASS DICEPHALOSOMATA** Sharov, 1966 (L. Camb. - U. Carb)

Pre-oral limbs raptorial, non cheliform, 4-14 segments; post-oral limbs non food-gathering; feeding pharyngeal, assisted by pre-oral limbs; trunk 12+ segmented, pygidial?; limbs locomotory, respiratory; aquatic.

†**CLASS ANOMALOCARIDEA** Raymond, 1935 (L. - M. Camb.)

Pre-oral limbs paired, 7-14 segmented; 1-3 post-oral head segments; peribuccal teeth present.

†**SUBCLASS ANOMALOCARIDATA** new (L. - M. Camb)

Pre-oral limbs 11-14-segmented; 3 post-oral head segments; trunk limbs natatory

†**Order Anomalocarida** Raymond, 1935 (*Anomalocaris* Whiteaves, 1892; ?*Hurdia* Walcott, 1912)

†**SUBCLASS CASSUBIATA** new (L. Camb)

Pre-oral limbs 7-segmented; 1? post-oral head segment; anterior trunk limbs ambulatory?

†**Order Cassubiida** new (*Cassubia* Lenzion, 1977)

†**CLASS PROTOCHELICERATA** Størmer, 1944, revised and restricted (L. - M. Camb.)

Pre-oral limbs paired, semi-chelicerate, 4-5 segmented; 3 pairs post-oral, biramous ambulatory head limbs.

†**SUBCLASS YOHOOIDACEA** Henriksen 1928, new status (L. - M. Camb)

Trunk limbs biramous, natatory, respiratory.

†**Superorder Yohoiidea** Henriksen 1928

†**Order Jianfengiiida** new (*Jianfengia* Hou, 1987) (L. Camb)

†**Order Yohoiida** Henriksen 1928 (*Yohoiia* Walcott, 1912) (M. Camb)

†**CLASS PROBOSCIFERIDEA** Sharov, 1966 emend (M. Camb - U. Carb)

Pre-oral limbs fused to clawlike (14-segmented) jaws on anterior proboscis; post-oral head segments and peribuccal teeth lacking.

†**SUBCLASS OPABINIIDACEA** Størmer, 1944 (M. Camb)

†**Order Opabiniida** Størmer, 1944 (*Opabinia* Walcott, 1912; ?*Kerygmachela* Conway Morris *et al.* 1987)

†**SUBCLASS TULLIMONSTRIDEA** E. L. Smith "Atlas" (U. Carb)

†**Order Tullimonstrida** (*Tullimonstrum* Richardson, 1966)

†**SUPERCLASS TRILOBITOMORPHA** Størmer, 1944, restricted status (L. Camb. - M. Perm.)

Pre-oral limbs filamentous, non raptorial; post-oral head limbs and trunk limbs normally biramous, endopods modified for food-gathering and/or feeding.

†**CLASS (SUBCLASS) LEANCHOILIIDACEA** Raymond, 1953, new status (L. - U. Camb.)

2-3 pairs post-oral, spinose (or weakly gnathobasic) transitional head limbs; trunk limb endopods transitional; telson large.

†**Superorder Leancoiliidea** Raymond, 1935

Head with 2 post-oral segments; pre-oral limbs multi-flagellate; eyes lacking.

†**Order Leancoiliida** (*Leancoilia* Walcott, 1912; *Acanthomeridion* Hou, Chen & Lu, 1989)

†**Superorder Alalcomenaeidea** Simonetta, 1970

Head with 3 post-oral segments; pre-oral limbs bi-flagellate or with accessory lobe; eyes present.

†**Order Actaeida** (*Actaeus* Simonetta, 1970)

†**Order Alalcomenaeida** (*Alalcomenaeus* Simonetta, 1970;

†**CLASS (SUBCLASS) SIDNEYIDEA** Walcott, 1911, new status (M. Camb.)

Lacking post-oral head segment(s) or limbs; trunk not trilobate, limbs gnathobasic; telson flabellate.

†**Order Limulavida** Walcott, 1911. (*Sidneyia* Walcott, 1911) (*Saratrocercus* - a larval stage?)

†**CLASS TRILOBITOIDEA** Størmer, 1955, restricted (L. Camb. - U. Perm.)

3 pairs of post-oral gnathobasic, masticatory head limbs; trunk limbs biramous, endopods gnathobasic.

†SUBCLASS BURGESSIDEA Walcott, 1912 (L. - M. Camb)

Trunk lacking lateral pleurae, limbs biramous; tail region with spikelike telson.

†Order *Burgessiida* Walcott, 1912 (*Burgessia* Walcott, 1912)

†Order *Molariida* Walcott, 1912 (*Molaria* Walcott, 1912; *Emeraldoides* Simonetta, 1964)

†Order *Habeliida* Simonetta & delle Cave 1972 (*Habelia* Walcott, 1912; *Thelxiopa*; *Economocaris*)

TRILOBITOIDEA INCERTAE SEDIS *Tontoia* Walcott, 1912. *Nathorstia* Walcott, 1912; *Retifacies* Hou, Chen & Lu, 1989; *Koumaia* Hou, 1987; *Rhombicalvaria* Hou, 1987; *Helmetia* Walcott, 1917; *Mollisonia* Walcott, 1912; *Urokodia* Hou, Chen & Lu, 1989; *Corcorania* Jell, 1980; *Serracaris* Briggs, 1978?

†SUBCLASS TRILOBITA Walch, 1771 (L. Camb - U. Perm)

Trunk segments typically with lateral pleurae (trilobate); tail region pygidial.

†Superorder *Eotrilobitacea* Whittington, 1977 (L. - M. Camb)

†Order *Nectaspida* Raymond, 1920 (*Naraoia* Walcott, 1912) (Incl. *Liwia* & *Tegopelte*, L. Camb)

†Superorder *Trilobitacea* Walch 1771 (L. Camb - M. Perm)

†Order *Agnostida* Kobayashi 1935

†Order *Redlichiida* Richter, 1933

†Order *Corynexochida* Kobayashi, 1935

†Order *Ptychopariida* Swinnerton 1915

†Order *Phacopida* Salter, 1964

†Order *Lichida* Moore, 1959

†Order *Odontopleurida* Whittington, 1959

†CLASS EMERALDELLIDEA Raymond, 1935 (M. Camb. - L. Dev.)

5 pairs of post-oral, gnathobasic, masticatory head limbs; trunk limbs biramous, endopods ambulatory.

†SUBCLASS SANCTICARIDEA E. L. Smith "Atlas" (M. Camb)

Pre-oral limb biramous; post-oral head limbs raptorial, unlike ambulatory trunk limbs; telson flabellate.

†Order *Sanctacarida* E. L. Smith "Atlas" (*Sanctacaris* Briggs & Collins, 1988 [= *Utahcaris orion* Conway Morris & Robison, 1988]).

†SUBCLASS EMERALDELLACEA Raymond, 1935 (M. Camb - L. Dev)

Pre-oral limb uniramous, filiform; post-oral head and trunk limbs ambulatory and raptorial; telson a spike

†Order *Emeraldellida* Simonetta & Della Cave, 1975, revised (*Emeraldella* Walcott, 1912)

†Order *Cheloniellonida* Brioli, 1933 (*Cheloniellon* Brioli, 1932) (L. Dev)

†Order *Aglaspida* (Walcott, 1911) (*Aglaspis* Hall, 1862, revised Briggs et al, 1978) (L. Ord)

Inclusions: *Aglaspella*, *Beckwithia*, *Palaeomerus*; *Borchgrevinkium*; *Palaeoniscus*, *Kodymirus*? *Strabops*?

SUPERCLASS CHELICERATA Heymons 1901 (L. Ord - R)

Pre-oral limb chelicerate, 3- (occasionally 2- or 4-) segmented; 5 (6) pairs of uniramous post-oral head limbs; trunk limbs uniramous, respiratory.

CLASS MEROSTOMATA Dana, 1852 (L. Ord - R)

Post-oral head limbs gnathobasic, first pair undifferentiated; trunk limbs reduced to book gills; aquatic.

SUBCLASS XIPHOSURA Latreille 1802 (L. Ord -R)

Pre- and post-abdomen strongly differentiated; one pair of compound eyes.

Superorder Chasmataspididea Caster & Brooks, 1956, revised status (L. Ord - Dev)

Post-abdomen 9-segmented; pre-abdomen 3-segmented?

Order Chasmataspidida Caster & Brooks, 1950 (L. Ord-Sil) (*Chasmataspis*, *Pseudoniscus*)

Order Diploaspidida Caster & Brooks, 1956 revised status (Dev) (*Diploaspis*, *Heteroaspis*)

Superorder Xiphosuridea Latreille, 1802 (U. Sil. - R)

Post-abdomen 1-3-segmented; pre-abdomen 7(8)-segmented.

†Order *Triopida* Packard, 1886 (L. Ord) (*Triopus*)

†Order *Synxiphosurina* Packard, 1886 (incl. *Weinbergina*) (6 pairs post-oral head limbs)

Order Limulina Richter & Richter, 1929 (Carb - R) (*Limulus* L. 1787; + *Euproops* (Carb))

†SUBCLASS EURYPTERIDA Burmeister, 1843 (L. Ord - Perm)

Pre and post-abdomen not strongly demarcated; 2 pairs compound eyes

†Order Eurypterida Burmeister, 1843 (*Eurypterus*)

†Order Pterygota Clarke & Rudemann, 1912

CLASS ARACHNIDA Lamarck 1801 (Ord. - R)

Post-oral head limbs (secondarily) non-gnathobasic, first often differentiated as pedipalps; feeding chelicerate; anterior trunk limbs forming book lungs or lacking; terrestrial.

SUBCLASS SCORPINIATA Latreille, 1817 (Sil - R)

Order Scorpionida Latreille 1806 (Sil - R)

SUBCLASS PEDIPALPATA Latreille 1906 (M. Dev - R)

Order Palpigradida Thorell, 1881 (Jur - R)

Order Schizomida Petrunkevitch, 1945 (U. Tert - R)

Order Uropygida Thorell, 1882 (U. Carb - R)

Order Amblypygida Thorell 1883 (U. Carb - R)

Order Aranaea Clerck, 1757 (U. Carb - R)

†Order Trigonotarbita Petrunkevitch, 1949 (M. Dev - U. Carb)

SUBCLASS PHALANGIATA Leach, 1915 (U. Carb - R)

Order Solfugida Leach 1815 (U. Carb - R)

Order Acarida Nitzsch 1818 (M. Dev - R)

Order Ricinulida Thorell, 1892 (U. Carb - R)

Order Opilionida Sundevall 1833 (U. Carb - R)

Order Pseudoscorpionida Latreille, 1817 (Olig. - R)

CLASS PYCNOGONIDA Latreille, 1910 (L. Dev - R)

Post-oral head limbs non-gnathobasic, first differentiated as pedipalps; feeding pharyngeal, pre-oral limb assisted; aquatic.

†SUBCLASS PALAEOPYCNOGONIDA E. L. Smith "Atlas" (L. Dev)

†Order Palaeoisopida Hedgepeth, 1978 (*Palaeoisopus* Broili, 1928)

†Order Palaeopantopoda Broili, 1930 (*Palaeopantopus* Broili, 1928)

SUBCLASS PODOSOMATA Leach, 1813 (L. Dev - R)

Order Pantopoda Gerstaecker, 1963 (*Pycnogonum littorale* L.)

TABLE IV. SUGGESTED NATURAL CLASSIFICATION OF BIANTENNATE ARTHROPODS

2. INFRAPHYLUM BIANTENNATA Bergström, 1979 revised (= MANDIBULATA Clairville, 1798)

Head with acron and 2 pairs of positionally pre-oral limbs, 2nd pair embryonically post-oral, biramous; 3rd (when present) mandibulate; trunk limbs not gnathobasic.

†SUPERCLASS EUTHYCARCINOMORPHA Handlirsch, 1914, revised status (L. Camb. - Trias)

Head 2(3)-segmented; head shield not maxillary; trunk tagmatized; thoracic limbs primitively biramous, endopods slender, multi-segmented, lacking terminal claws; abdomen limbless, with telson..

†CLASS EUTHYCARCINOIDEA Handlirsch, 1914 (L. Camb - U. Trias)

With the characters of the superclass.

†SUBCLASS FUXIANHUIATA new (L. Camb)

Trunk multi-segmented, segments simple, each with one pair of biramous limbs; telson short.

†Order Fuxianhuiida new (*Fuxianhuia protensa* Hou, 1987)

INCERTA SEDIS: *Chengjiangocaris longiformis* Hou & Bergström, 1991.

†SUBCLASS EUTHYCARCINATA Handlirsch, 1914. (U. Carb - Trias)

Trunk with few (<20) diplo- and/or triplo- segments; trunk limbs uniramous, two per diplo-segment; telson elongate.

†Order Sottixeriformes Schram & Rolfe, 1982 (*Pieckoxerxes piekoe* Starobogatov, 1988)

†Order Euthycarciniformes Schram & Rolfe, 1982 (*Kottixerxes gloriosus* Starobogatov, 1988)

†**SUPERCLASS MARRELLOMORPHA** Walcott, 1912, new status (M. Camb - L. Dev)

Head 2-4-segmented; head shield spinose or bivalved, not maxillary; mandible, endopod leglike; trunk not tagmatized; trunk limbs undifferentiated, endopods strongly leglike, ambulatory, exopods narrowly lamellate.

†**CLASS MARRELLIDEA** Walcott, 1912 (M. Camb - L. Dev)

Head 2-3 segmented; head shield with paired spines; telson minute.

†**SUBCLASS MARRELLATA** Walcott, 1912 (M. Camb)

Head 2-segmented; first post-oral head limbs antenna-like.

†**Order Marrellida** Walcott, 1912 (*Marrella* Walcott, 1912)

†**SUBCLASS MIMETASTERATA** E. L. Smith "Atlas" (L. Dev)

Head 3-segmented; first post-oral head limbs leg-like.

†**Order Mimetasterida** (*Mimetaster* Gurich, 1931)

†**CLASS ACERCOSTRACA** Lehmann, 1955 (L. Dev)

Head 4-segmented; head shield with carapace.

†**SUBCLASS VACHONISIATA** E. L. Smith "Atlas" (L. Dev)

Post-oral limbs 3 & 4 leglike, weakly gnathobasic.

†**Order Vachonisiida** new (*Vachonisia* Lehmann, 1955)

†**SUPERCLASS PHYLLOPODA** Latreille, 1825 revised, restricted (M. Camb - L. Ord)

Head 3-segmented; head shield bivalved, not maxillary; mandible masticatory, not leglike or palpate; trunk 15+ segmented, weakly tagmatized; endopods weakly leglike, exopods broadly lamellate (phyllopodous).

†**CLASS BRANCHIOCARIDEA** E. L. Smith "Atlas" (M. Camb)

Head 3-segmented; trunk segments numerous (20+), with similar phyllopodous limbs.

†**SUBCLASS BRANCHIOCARATA** E. L. Smith "Atlas" (M. Camb)

First two pairs of head appendage prominent, 2nd pair cheliform?; carapace normal; tail region bifid.

†**Order Branchiocarida** E. L. Smith "Atlas" (*Branchiocaris* Briggs, 1976)

†**SUBCLASS ODARAIATA** Simonetta & Delle Cave, 1975 (M. Camb)

Pre-oral appendages minute, linear?; carapace tubular; tail region trifid.

†**Order Odaraiida** Simonetta & Delle Cave, 1975 (*Odaraia* Walcott, 1912)

†**CLASS (SUBCLASS) CANADASPIDIDEA** Novosilov, 1960 (M. Camb - L. Ord)

Head appearing indistinctly 5-segmented, posterior 2 pairs of limbs similar to trunk limbs; trunk 15-segmented, posterior 7 segments lacking paired appendages.

†**Order Canadaspidida** (*Canadaspis* Novosilov, 1960; *Perspicaris* Briggs, 1977; ?*Rhebachella kinnekullensis* Müller 1983 (larval stages)

?**Order Hymenotraca** Rolfe, 1969 (*Hymenocaris* Salter, 1853) (M. Camb - L. Ord)

SUPERCLASS CRUSTACEA Pennant, 1777 (after Schram, 1986) (M. Camb - R)

Head with pre-oral antenna and 4 post-oral limbs, first antennalike, 2-4 (including mandible) masticatory; head shield maxillary; trunk often tagmatized, limbs often differentiated, specialized; telson present.

CLASS (SUBCLASS) REMIPEDIA Yager, 1981 (M. Dev - R)

†**Order Enantiopoda** Birshtein, 1960 (*Tesnusocaris* Brooks, 1955) (M. Dev)

Order Nectiopoda Schram, 1986 (*Speleonectes* Yager, 1981) (R)

CLASS BRANCHIOPODA Latreille, 1817 (L. Dev - R)

SUBCLASS SRSOSTRACA Tasch, 1969 (M. Dev - R)

†**Order Lipostraca** Scourfield, 1926 (M. Dev)

Order Anostraca Sars, 1867 (L. Dev - R)

SUBCLASS CALMANOSTRACA Tasch, 1969 (M. Dev. - R)

Order Notostraca Sars, 1867 (L. Dev - R)

Order Kazacharthrac Novozhilov, 1957 (L. Jur)

Order Conchostraca Sars, 1867 (L. Dev - R)

Order Cladocera Latreille, 1829 (Perm - R)

CLASS (SUBCLASS) CEPHALOCARIDA Sanders, 1955 (R)

Order Brachypoda Birshtein, 1960 (*Hutchinsoniella* Sanders, 1955)

CLASS MAXILLOPODA Dahl, 1956 (L. Camb - R)

†**SUBCLASS SKARACARIDA** Müller, 1983 (M. Camb - U. Camb))

Order Skaracarida Müller, 1983. *Skara annulata* Müller, 1983) (several other, mostly larval genera, e.g., *Dala*, *Walossekia*, *Oelandocaris*, *Bredocaris*,

SUBCLASS OSTRACODA Latreille, 1836 (L. Camb - R)

†**Order Bradoriidae** Matthew, 1902

†**Order Phosphatocopida** K. J. Müller, 1964 (L. Camb. - L. Ord)

†**Order Leperditicopida** Scott, 1961 (U. Camb - U. Dev)

†**Order Palaeocopida** Henningsmoen, 1953 (L. Ord - Trias)

Order Halocyprida Dana 1852 (Sil - R)

Order Platycopida Sars 1866 (L. Ord - R)

Order Cladocopida Sars 1866 (Ord - R)

Order Myodicopida Sars, 1966 (Ord - R)

Order Podocopida Sars, 1866 (Sil - R)

SUBCLASS THECOSTRACA Gruvel, 1905 (M. Camb - R)

Order Facetotecta Gruvel, 1905

Order Rhizocephala F. Müller, 1862

Order Ascothoracida Lacaze-Duthiers, 1880

Order Cirripedia Burmeister, 1834 (M. Camb - R)

SUBCLASS TANTULOCARIDA Boxshall & Lincoln, 1983 (R)

Order Tantulocaridida Boxshall & Lincoln, 1983

SUBCLASS COPEPODA Milne-Edwards, 1840 (Cret - R)

Order Calanoida Sars, 1903

Order Harpacticoida Sars, 1903

Order Cyclopoida Burmeister, 1834

Order Misophrioida Gurney, 1933

Order Monstrilloida Sars, 1903

Order Siphonostomatoida Thorell, 1859 emend Sars 1918

Order Poecilostomatoida Thorell 1859

SUBCLASS LINGULATULIDA Frolich, 1789 (=Pentastomatida Rudolphi 1819) (R)

Order Cephalobaeniuda Heymons & Vitzthum, 1936

Order Porocephalida Heymons & Vitzthum, 1936

†**CLASS (SUBCLASS) THYLACOCEPHALA** Pinna, Arduini *et al.*, 1982. (Camb? L. Sil - Cen)

†**Order Concavicularia** Briggs & Rolfe, 1983 (L. Sil - Cen)

†**Order Conchyliocarida** Secretan, 1983 (Camb? - Jur)

CLASS MALACOSTRACA Latreille 1806 (Dev - R)

SUBCLASS PHYLLOCARIDA Packard, 1879 emended (Dev - R)

†**Order Archaeostraca** Claus, 1888

†**Order Hoplostraca** Schram, 1973

Order Leptostraca Claus, 1880 (see also Dahl, 1984)

SUBCLASS HOPLOCARIDA Calman 1904 (U. Dev - R)

†**Order Aeschronectida** Schram, 1969 (Carb)

†**Order Palaeostomatopoda** Brooks, 1955 (U. Dev - L. Carb)

Order Stomatopoda Latreille, 1817 (Carb - R)

SUBCLASS EUMALACOSTRACA Grobben, 1892 (modified from Schram, 1986) (U. Dev - R)

Superorder Syncarida Packard, 1885 (U. Carb - R)

†**Order Palaeocaridacea** Brooks, 1962

- Order Anaspidacea** Calman, 1904
Order Bathynellacea Chappuis, 1915
Order Stygocaridacea Noodt, 1964
 †**Superorder Belotelsonidea** Schram, 1981
 †**Superorder Waterstonellidea** Schram, 1981
 †**Superorder Eocaridacea** Brooks, 1962
Superorder Thermosbaenacea Monod, 1927
Superorder Mysidacea Boas, 1883
Order Lophogastrida Boas, 1883
 †**Order Pygocephalomorpha** Beurlen, 1930
Order Mysida Boas 1883
Superorder Amphipoda Latreille, 1916
Superorder Hemicaridea Schram, 1981 emended
Order Spelaeogriphacea Gordon, 1957
Order Mictacea Bowman et al. 1985
Order Cumacea Kroyer, 1846
Order Tanaidacea Dana, 1853
Superorder Isopoda Latreille, 1817
Superorder Eucarida Calman, 1904
Order Euphausiacea Dana, 1862
Order Amphionidacea Williamson, 1973
Order Decapoda Latreille, 1803
SUPERCLASS MYRIAPODA Latreille, 1796 (Sil - R) (Essentially terrestrial; not detailed here)
 Head with embryonic acron, pre-oral antenna, 5 post-oral pairs of masticatory limbs (1st post-oral embryonic); trunk not tagmatized, with more than 20 pairs of ambulatory limbs, ending in telson.
CLASS SYMPHYLA Ruder, 1880 (1 subclass) (Olig - R)
CLASS CHILOPODA Latreille, 1802 (2 subclasses) (M. Dev - R)
CLASS PAUROPODA Lubbock, 1866 (1 subclass) (R)
CLASS DIPLOPODA Gervais, 1844 (3 subclasses) (Sil - R)
 †**CLASS ARTHROPLEURIDEA** Zittel, 1848 (1 subclass) (L. Dev - U. Carb)

SUPERCLASS HEXAPODA (L. Dev. - R.) (Essentially terrestrial; not detailed here)
 Head with acron + pre-oral antenna, 4 post-oral pairs masticatory limbs (1st post-oral embryonic, 2nd mandibulate; trunk tagmatized; thorax with 3, abdomen with 11 (max.) pairs ambulatory limbs; telson embryonic.
CLASS PARINSECTA (2 Subclasses: *Collembola*, *Protura*) (L. Dev - R)
CLASS INSECTA (2 Subclasses *Entognatha*, *Ectognatha*) (U. Carb - R).

TABLE V. NUMBERS OF HIGHER ARTHROPOD TAXA SINCE CAMBRIAN TIMES.

ARTHROPOD INFRAPHYLA	P E R I O D									IV TOTALS		
	I CAMBRIAN (545-495 mybp)			II LATE PALEO- ZOIC (~300 mybp)			III TERTIARY- RECENT (0-30 mybp)					
	SPCL.	CL.	SBCL.	SPCL.	CL.	SBCL.	SPCL.	CL.	SBCL.	SPCL.	CL.	SBCL.
	UNIAN TENNATA	2	8	11	3	5	8	1	3	5	3	10
BIAN TENNATA	4	6	9	5	11	24	3	12	24	6	18	34
TOTAL ARTHROPODA	6	14	20	8	16	32	4	15	29	9	28	52

Arthropod Diversity and Evolutionary Trends

Table V summarizes (from Tables III & IV) the number of higher arthropod taxonomic categories, recognized here at superclass (SPCL), class (CL) and subclass (SBCL) levels, that are represented by known genera and species of the Cambrian, late Paleozoic and Tertiary-Recent Periods. Analysis of the changing numbers with geological time reveals interesting and perhaps significant evolutionary trends.

Despite the very great difference in numbers of species known for each of the three time-scale samplings (Cambrian $\sim 10^2$ species; Late Paleozoic $\sim 10^4$ species; Tertiary-Recent $\sim 10^6$ species), the numbers of higher taxa are of comparable orders of magnitude for all categories. In the 600-million-year time span since the presumed dawn of arthropod life (Ediacrian, Vendian), we here categorize only 9 superclasses, 28 classes and 52 subclasses to encompass the entire known fauna, past and present, of well over one million described species (Table V, Col. IV, bottom row). Fully one-third of the early subclasses is known from only 1-10 species, a fact suggesting the likelihood of further new discoveries, at that level or higher, among incompletely described or totally new fossil material. Only one of the 9 superclasses (Crustacea), one of the 28 classes (Maxillopoda) and only two of the 52 subclasses (Ostracoda, Thecostraca) have actually been recorded throughout this immense paleontological range. To this meager total we might add the Chelicerata but it is presently confirmed not earlier than Lower Ordovician. However, further analysis of Paleozoic fossil material is expected to extend the time range of extinct species forwards, and recent species (especially minute, soft-bodied forms), backwards in time. Thus, the morphologically primitive Remipedia and Cephalocarida may have originated during Cambrian times, despite their very limited or non-existent fossil records (see Hessler, 1984). Aquatic larval stages of some other classes of Crustacea and of the merostomatid uniantennates (e.g., phyllocarid and trilobite larvae, respectively), tend to recapitulate adult morphology of extinct, but related, Cambrian categories.

Thus, by the Cambrian Period, 67% (6/9) of the superclasses, but only $\sim 50\%$ (14/28) of the classes and $\sim 38\%$ (20/52) of the subclasses had evolved. By the late Paleozoic, perhaps the heyday of arthropod evolution generally, nearly all (8/9) the superclasses, and $\sim 60\%$ (16/28; and 32/52) of all classes and subclasses were represented. Today, however, scarcely half (4/9 and 15/28) the superclasses and classes persist, and the percentage of subclasses, 56% (29/52), has also dropped slightly.

If trends are analysed according to infraphylum for each time interval, for the uniantennates the percentages were highest during the Cambrian, with 33% (2/6) of the superclasses, 57% (8/14) of the classes, and 55% (11/20) of the subclasses. However, the group decreased markedly in importance by the late Paleozoic (only 37% of superclasses, $\sim 31\%$ of classes, and $\sim 25\%$ of subclasses), and is lowest today (25% of superclasses, $\sim 20\%$ of classes, and only $\sim 17\%$

of subclasses). By contrast, the biantennates increased steadily from lowest values in the Cambrian (67% of superclasses, 43% of classes and 45% of subclasses), through the late Paleozoic (63% of superclasses, $\sim 70\%$ of classes, and $\sim 67\%$ of subclasses), to maximum dominance today (75% of superclasses, $\sim 80\%$ of classes, and $\sim 83\%$ of subclasses).

These changes in relative numbers of the two arthropod infraphyla may reflect the impact of the evolution of vascular plants during Silurian-Devonian and later periods (Kukalova-Peck, 1987). That event provided an enormous new food resource in both aquatic and terrestrial environments. These nutrients could be exploited by the omnivorous aquatic crustaceans and terrestrial myriapods and hexapods by direct adaptation and diversification of feeding morphology and style (as in malacostracan crustaceans, and winged insects). By contrast, the uniantennates were more or less "locked into" their mainly carnivorous, and some detritivorous life styles; they could take only indirect advantage of this food resource, and only by developing new predatory morphologies and life styles, especially within the terrestrial environment. They are now a secondary part of the terrestrial, and a minute relict part of the aquatic, arthropod fauna.

With respect to the level of arthropod disparity during Cambrian times, the positions of both Gould (1989) and proponents to the contrary (e.g., Ridley, 1993; Wills et al. 1994) receive support from the present analysis. Thus, of 9 "all-time" arthropod superclasses, 7 (including Chelicerata) were represented in Cambrian and Lower Ordovician faunas, but only 4 are represented in the Recent fauna. Especially remarkable is the fact that Cambrian arthropods were entirely aquatic, and were represented by less than 100 species from a very limited series of marine habitats. The two superclasses missing from the Cambrian record, the Myriapoda and the Hexapoda, are both essentially terrestrial. Thus, if only aquatic faunas are considered, the disparity level of Cambrian arthropods is more than 3 times greater (7 vs. 2 superclasses) than today.

On the other hand, at class level, disparity levels are similar (14 vs. 15), and at subclass level, the Recent arthropod fauna is about 50% richer (29 vs. 20). Furthermore, all of the arthropod, or arthropodlike, species of the Burgess Shale, designated by Gould (1989) and Briggs et al. (1993) as new (or probably new) at phylum and/or infraphylum levels, can be adequately encompassed within existing class and/or superclass categories.

Thus, it is concluded here that, during the entire evolutionary history of the Arthropoda, disparity levels were at or near maximum during the Cambrian Period. Such a high level, close to the starting point of the arthropod fossil record, is consistent with the probable correctness of the evolutionary theory of punctuated equilibrium (Eldridge & Gould, 1972). Since invertebrate faunas of early "explosive evolutionary" times were not described comprehensively until the early 20th century (e.g., Walcott (1912), and later), Charles Darwin (1859) may be excused for missing that part of the evolutionary story.

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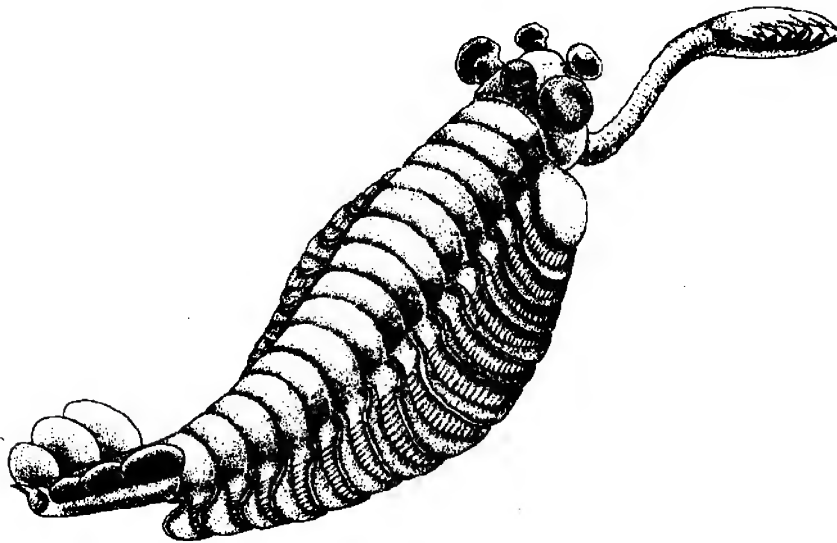
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Opabinia regalis Walcott

Middle Cambrian Arthropod

(Marianne Collins illustration,
modified from Gould, 1989)

**THE AMPHIPOD SUPERFAMILY PONTOPOREIOIDEA ON THE PACIFIC COAST OF NORTH AMERICA.
I. FAMILY HAUSTORIIDAE. GENUS *Eohaustorius* J. L. BARNARD: SYSTEMATICS AND
DISTRIBUTIONAL ECOLOGY**

by E. L. Bousfield¹ and Phillip Hoover²

ABSTRACT

On the Pacific coast of North America, from the Bering Sea to Southern California, the free-burrowing gammaridean amphipod family Haustoriidae is represented by six species of *Eohaustorius* Barnard, 1957. On the Asiatic Pacific coast six species, all subtidal, have now been described. A single northern subtidal species, *E. eous*, connects the two faunas in the Bering Sea region.

This paper describes *E. barnardi*, new species, from off Pt. Conception, California, and provides re-descriptions, keys and new distributional information for *Eohaustorius eous* (Gurjanova, 1951), *E. estuarius* Bosworth, 1973, *E. sawyeri* Bosworth, 1973, *E. brevicuspis* Bosworth, 1973, *E. sencillus* Barnard, 1962 and *E. washingtonianus* (Thorsteinson, 1941). Material ascribed to the latter species from the northwestern Pacific region by Gurjanova (1962) is herewith redescribed as *E. gurjanovae*, new species. Subtidal material from South Korea is described as *E. longicarpus*, new species.

The species of *Eohaustorius* are morphologically variable throughout their ranges, especially *E. washingtonianus*, but variation is not considered of species or subspecies value. Cluster analysis reveals three main subgroupings, none very closely inter- or intra-related, viz: a North American endemic group of *E. washingtonianus* Barnard, *E. brevicuspis* Bosworth and *E. barnardi*, new species; an Asiatic Pacific group of *E. cheliferus* Bulcheva, *E. subuliculus* Hirayama and *E. robustus* Gurjanova; and a northern relatively primitive core group of *E. eous* (Gurjanova), *E. sawyeri* Bosworth, *E. gurjanovae*, new species, *E. estuarius* Bosworth, *E. longicarpus*, new species, and *E. sencillus* Barnard. The Asiatic species have relatively restricted distributions and none is intertidal. This hiatus results presumably from competition with intertidal members of amphipod family Dogielinotidae dominant in that region, and from severe physical factors in winter of low intertidal temperatures and ice scour. On the North American Pacific coast, however, all species have relatively wide geographical ranges, and four species are intertidal. There, only one species of Dogielinotidae, *Probosciniotus loquax*, provides intertidal competition, and the climate is equable year-round winter ice scour is lacking.

The genus *Eohaustorius* is sufficiently similar to North American Atlantic haustorinid genera as to preclude separate evolution from a pontoporeiid ancestor and thereby render polyphyletic the family Haustoriidae. However, the genus *Eohaustorius* is cold-temperate, and the Atlantic-endemic genera are warm-temperate, in biogeographical affinities. *Eohaustorius* is closest morphologically to the Atlantic subtidal genus *Pseudohaustorius*, thereby raising the possibility that during early Miocene times, prior to emergence of the isthmus of Panama, a common ancestor connected the two groups via a southern marine waterway.

INTRODUCTION

The superfamily Pontoporeioidea is a relatively small group of fossorial amphipods, whose marine members are found mainly in sedimentary substrata along holarctic shores. Members of the primitive family Pontoporeiidae tend to be arctic and sub-arctic in distribution, with a significant component confined to glacial relict freshwater lakes of North America and northwestern Eurasia (Bousfield, 1987). By contrast, members of the advanced and highly specialized family Haustoriidae are marine and estuarine and occur mainly along warm-temperate and boreal coastlines of the North Atlantic and North Pacific regions (Bousfield, 1965; 1970, 1973). On the Pacific coast of North America, family Pontoporeiidae is sparsely represented (Bousfield, in prep: *Priscillina* and *Monoporeia* in the Bering Sea, *Pontoporeia* in glacial fjords, and *Diporeia* in a few post-glacial lake basins). However, owing mainly to the work of Thorsteinson

(1941), Gurjanova (1951, 1962), Barnard (1957, 1962), Bosworth (1973) and Coyle & Mueller (1981), the family Haustoriidae is known to be moderately speciose in shallow, high energy coastal marine waters from the Bering Sea coast of Alaska to southern California. The genus is well represented in coastal waters of Korea and Japan (Ishimarus, 1994), and along the Russian coast north to the Bering Sea region, but not in Arctic waters.

Within the North Pacific region generally, the family Haustoriidae is represented only by the single genus, *Eohaustorius* Barnard, 1957. Some seven species of this genus have been recorded from the North American Pacific coast and another five from the Pacific coast of Russia and the Japan Sea (including Korea). The genus is distinct from the North Atlantic complex (with the European species *Haustorius arenarius* (Slabber) as type) in having peraeopods 3 and 4 unlike in size and form, and telson lobes widely separated on the dorsum of urosome 6, among other differences.

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This study treats the systematics and distributional ecology of species of the genus *Eohaustorius* in North Pacific coastal marine region, and emphasizes the North American Pacifica fauna.

Species of *Eohaustorius* have proven useful as indicators of sediment quality (see Bousfield, 1991; Mcleay et al. (1990); Yee et al. 1992).

Acknowledgements. The present North American haustoriid material was accumulated mainly as a result of National Museum, now Canadian Museum of Nature (CMN), field expeditions, conducted by one of us (ELB) and colleagues, during the period 1955-1980. Complete lists of stations, pertinent data and acknowledgement of field assistance are provided elsewhere (Bousfield, 1958, 1963, 1968; Bousfield & McAllister, 1962; and Bousfield & Jarrett, 1981). Additional material was provided by Drs Peter Slattery, Moss Landing, California; Charles O' Clair, Auke Bay, Alaska; Kathleen Conlan CMN, Ottawa, and McLeay Associates, West Vancouver. The authors are most grateful for use of the laboratory facilities of Dr D. V. Ellis, University of Victoria, and for the use of collections and facilities of the CMN in Ottawa.

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SYSTEMATICS

Haustoriidae Stebbing

Haustoriidae Stebbing, 1906: 118.—Gurjanova, 1951: 328; 1962: 395.—Bousfield, 1965: 165 (part); 1973: 99 (part); 1982: 259.—Barnard and Drummond, 1982: 136.—Hirayama, 1985: 395.—Barnard & Karaman, 1991: 357.

Taxonomic commentary. Barnard and Karaman (1991) have provided a simplified key to genera of *Haustoriidae* (sensu strictu).

With respect to superfamily classification, Barnard & Karaman (loc. cit.) have continued recognition of family *Haustoriidae* as the type of superfamily *Haustorioidea*, proposed initially by Barnard & Drummond (1982). As shown by Bousfield (1982b, 1990) and Bousfield & Shih (1994), the Barnardian concept (of *Haustorioidea*) includes most members of family *Urothoidae* and other superficially and convergently similar families. The latter groups are phylogenetically more correctly placed within superfamily *Phoxocephaloidea* (e.g., Bousfield 1982, 1990; and Schram, 1986). In all major character states, family *Haustoriidae* is most clearly related to members of family *Pontoporeiidae*,

and thus phylogenetically assignable to the superfamily which the latter typifies, the *Pontoporeioidea*. As shown above (Bousfield, loc. cit.), these major pontoporeioidean character states of *Haustoriidae*, especially of its most primitive genus *Protohaustorius*, include its short broad, weakly rostrate head, "pseudorostrate" paired peduncles of antenna 1, weakly (or non-) dactylate peraeopods and maxilliped, lack of coxal gill on peraeopod 7, unique form of the pleopods (lacking clothespin spines), strongly deflexed urosome, and the holarctic (non-antipodean) distribution of nearly all member species. The character states of the *Pontoporeioidea*, especially the phylogenetically significant antennal calceoli, are basically gammaroidean and not phoxocephaloidean or crangonyctoidean in form.

Eohaustorius J. L. Barnard

Eohaustorius J. L. Barnard, 1957: 81.—Gurjanova, 1962: 400.—Bousfield, 1970: 150.—Bosworth, 1973: 160.—Barnard, 1975: 348 (key).—Hirayama, 1985: 43.—Barnard & Karaman, 1991: 361.—Ishimaru, 1994: 64.

Type species. *Haustorius washingtonianus* Thorsteinson, 1941, original designation.

Component species. *E. tandeensis* Dang, 1968; *E. subuliculus* Hirayama, 1985; *E. cheliferus* (Bulycheva, 1952); *E. eous* (Gurjanova, 1951); *E. robustus* (Gurjanova, 1953); *E. sawyeri* Bosworth, 1973; *E. brevicuspis* Bosworth, 1973; *E. estuarius* Bosworth, 1973; *E. longicarpus*, new species; *E. gurjanovae*, new species; *E. sencillus* Barnard, 1962; *E. barnardi*, new species.

Diagnosis. Body short, broad. Head broad; rostrum short, acute. Pigmented eyes essentially lacking. Antenna 1, flagellum 5-segmented; accessory flagellum 2-segmented, attached subapically to peduncular segment 3, bearing aesthetascs. Antenna 2, peduncle 4 broadly lobate and strongly setose behind; peduncle 5 broad, not lobate behind; flagellum 4-5 segmented.

Upper lip rounded. Lower lip, inner lobes with short proximal processes. Mandible, molar strong tritritative; incisor acute; palp segment 3 with few (5-15) inner marginal comb spines. Maxilla 1 lacking accessory basal baler lobe; inner plate with single apical seta; outer plate with 8-9 apical spines. Maxilla 2, outer plate little larger than inner, not lunate in form; inner plate with weak facial setae. Maxilliped, inner plate with 2 apical spines; outer plate very large, exceeding palp segment 2; palp segment 3 clavate, not geniculate.

Coxal plates 1 & 2 small, 3 & 4 squarish below. Gnathopod 1, segment 3 very short; segment 5 relatively short, deep; segment 6 medially deepest. Gnathopod 2, segment 3 very short; segment 5 with postero-distal cluster of specialized spines; segment 6 short, medially swollen, arcuate, produced beneath minute dactyl to form a microchela.

KEY TO NORTH PACIFIC SPECIES OF *EOHAUSTORIUS*

1. Pleon plate 3 strongly produced behind into a recurved hooklike process; peraeopod 4, hind lobe of segment 5 elongate, slender, length 4-5 X width (depth); uropod 3, inner ramus with single small inner marginal seta; Asiatic coast. *E. subuliculus* (p. 42)
 —Pleon plate 3, hind process nearly straight, if hooked, not recurved; peraeopod 4, segment 5, hind lobe shorter, deeper, length less than 2 X depth; uropod 3, inner margin with 2-6 setae 2.
2. Peraeopod 6, segment 4 tall, length 2X width, with 5-6 groups of facial spines (in addition to marginal spines); basis slender, distinctly narrower than length (depth), subovate; uropod 1, hind margin of inner ramus with 2 single setae; gnathopod 1, dactyl, body large, length > nail (unguis) 3.
 —Peraeopod 6, segment 4 subtriangular, widest distally, length < 2X width; basis as broader or broader than length; gnathopod 1, dactyl, nail longer than body. 4.
3. Antennae 1 & 2, flagella 5-segmented; peraeopod 4, hind lobe elongate, ~2 X depth; abdominal side plate 3, apex abruptly upturned, minutely split-tipped *E. longicarpus* (p. 56)
 —Antenna 1 & 2, flagella 3-segmented; peraeopod 4, segment 5, hind lobe short, length not greater than depth; abdominal side plate 3, hind process straight or apex slightly upturned *E. sencillus* (p. 44)
4. Peraeopod 4, segment 5, posterior lobe, distal margin with spine cluster; peraeopod 6, segment 4 with lower facial row of 2-3 spine groups; peraeopod 6, segment 5 with posterior marginal spine group . . . 7.
 —Peraeopod 4, segment 5, distal lobe base, smooth; peraeopod 6, segment 4 with at least one other spine cluster above lower row; peraeopod 6, segment 5 lacking posterior marginal spines 5.
5. Peraeopod 7, basis, hind margin proximally with strong cusp or tooth; pleon plate 3 produced, posteriorly as weak tooth *E. washingtonianus* (p. 50)
 —Peraeopod 7, basis hind marginal tooth weak or rounded; pleon plate 3, process strong 6.
6. Peraeopod 7, basis wider than deep, hind cusp rounded; maxilliped palp, segment 3 strongly broadened distally, width = 3/4 length *E. brevicuspis* (p. 50)
 —Peraeopod 7, basis not wider than deep, hind cusp acute; maxilliped palp, segment 3 normal, length ~2X width *E. barnardi* (p. 54)
7. Peraeopod 4, segment 5, hind lobe strongly produced, width of segment 2 X depth (length); peraeopod 7, segment 6 with 2 posterior marginal groups of spines; gnathopod 2, basis, hind margin with distal setae only *E. cheliferus* (p. 55)
 —Peraeopod 4, segment 5, hind lobe normal, width about equal to length; peraeopod 7, segment 6 with 3-4 posterior marginal spines groups; gnathopod 2, basis, hind margin setose throughout 8.
8. Peraeopod 5, segment 4 widest distally, 2X length; pleon plate 3, postero-dorsal process large, strongly overhanging urosome; uropod 3, inner ramus with 2-3 marginal setae *E. sawyeri* (p. 44)
 —Peraeopod 5, segment 4 less broad, ~ 1.5X length; pleon overhang normal, little or not exceeding side plate process; uropod 3, inner ramus with 5 marginal setae 9.
9. Peraeopod 7, segment 6 with 2 groups of posterior marginal spine groups; coxae 3 & 4 antero-distal margins rounded *E. estuarius* (p. 40)
 —Peraeopod 7, segment 6 with 3-4 posterior marginal spine groups; coxae 3 & 4 squarish 10.
10. Peraeopod 5, segment 6 with 1 group of anterior marginal spines; pleon plate 3, hind process, apex slightly upturned; peraeopod 4, segments 5 & 6 lacking anterior marginal spines; peraeopod 7, basis very broad, exceeding length *E. robustus* (p. 48)
 —Peraeopod 5, segment 6 with 2 groups anterior marginal spines; pleon plate 3 hind process straight; peraeopod 4, segment 5 & 6 with anterior marginal spines; peraeopod 7, basis not wider than deep 11.

11. Peraeopod 7, segment 6 with 4 posterior marginal spines; basis lacking posterior cusp; mandibular palp segment 3 with 14-15 posterior marginal comb spines *E. eous* (p. 38)
 —Peraeopod 7, segment 6 with 3 posterior marginal spines; basis with rounded posterior proximal cusp; mandibular palp segment 3 with 8-9 posterior marginal comb spines *E. gurjanovae* (p. 47)

Peraeopod 3, segment 4 short, triangular; 5 weakly lobate behind; 6 small, margins spinose, not setose. Peraeopod 4 smaller and unlike peraeopod 3 in form; segment 3 very short, 4 little broadened, 5 strongly produced and spinose behind; 6 slender, distally spinose and setose.

Peraeopod 5, basis broad, hind margin setose, with proximal cusp; segments 4-6 not broader than long, outer face with spine clusters. Peraeopod 6 longest; basis medium broad, hind margin setose, with proximal cusp; segment 4 often longer than broad; segment 5 broader than long, with prominent antero-distal process and distal marginal notch; segment 6, some distal spines split-tipped. Peraeopod 7, basis very broad hind margin nearly bare, proximal cusp low or lacking; segment 4 broad, triangular; segment 5 broad.

Pleon segment 3 strongly deflexed posteriorly, postero-distal lobe strong, overhanging urosome. Pleon plate 3, hind corner acutely produced. Pleopods powerful; peduncle short, broad; outer ramus 10-16 segmented, inner shorter, with proximal baso-medial lobe.

Urosome short, lacking antero-distal lappet. Uropod 1, rami cylindrical, inner ramus with posterior marginal setae only. Urosome 2 short, not occluded dorsally. Uropod 2, rami heavily setose, subequal. Uropod 3, rami short, <2X peduncle, terminal segment variable. Telson lobes widely separated at base; each with dorso-lateral marginal setae, and single apical penicillate seta.

Coxal gills saclike, on peraeopods 2-6. Brood plates relatively narrow, elongate.

Distribution. Member species are endemic to the North Pacific coastal shelf regions of eastern Asia, and North America, from the Bering Sea to Vietnam in the west, and in the east, south to Baja California.

Taxonomic commentary. *Eohaustorius* is distinct from North American Atlantic genera in the unlike form of peraeopods 3 & 4 and the widely separated telson lobes. However, in the short antennal flagella, form of the lower lip, maxilla 1 & 2, maxilliped, processiferous pleon plate 3, and setose telson, it more closely resembles the warm-temperate North Atlantic genus *Pseudohaustorius* (Fig. 2, p. 41) than the type genus *Haustorius* (Fig. 2.2). Such basic similarities suggest a former ancestral link with the diverse Atlantic haustoriid complex via the submerged Panama isthmus (Bousfield, 1970) (see also pp. 61-62).

Eohaustorius eous (Gurjanova)
 (Figs. 1, 2)

Haustorius eous Gurjanova, 1951: 331.

Eohaustorius eous eous Gurjanova, 1962: 406.

Eohaustorius eous Barnard & Karaman, 1991: 463.—Ishimaru, 1994: 64.

LEGEND FOR FIGURES

A1	-	antenna 1	MX 1	-	maxilla 1
A2	-	antenna 2	MX2	-	maxilla 2
BR.	-	coxal gill	MXPD	-	maxilliped
BR SET	-	brood plate seta	O. P.	-	outer plate
COXAE	-	coxal plates	PLP	-	palp
DACT	-	dactyl	P3-P7	-	peraeop'ds 3-7
EP 1-3	-	pleon plates 1-3	RT	-	right
GN1	-	gnathopod 1	SP	-	spine
GN2	-	gnathopod 2	T	-	telson
I. P.	-	inner plate	U1-U3	-	uropods 1-3
I. R.	-	inner ramus	UROS	-	urosoma
LFT	-	left	X	-	magnified
LL	-	lower lip	o	-	male
MD	-	mandible	o	-	female

Material examined.

ALASKA. Bering Sea: Northeast end of St. Lawrence I., Lot #1, 20 m sand, P. Slattery coll., July 10, 1980 - 2 males, 4 females, 1 im, CMN Cat. no. NMCC1991-1209; *Ibid.*, Lot #5 - 2 males, 13 female, 5 im.

St. Mathew I., Walrus Cove, sand, 8 m, P. Slattery coll., 1983 - 1 im; *Ibid.*, 11 m scoop, sand - 3 males, 11 females, 2 im; *Ibid.*, 13 m, sand - 2 males, 21 females, 14 im. CMN Cat. no. NMCC1991-1206.

St. Paul I., English Bay, 3 m scoop, P. Slattery coll., 1983, - 5 males, 37 females, 8 im; *Ibid.*, 10 m sand - 3 males, 9 females, 2 im; *Ibid.*, reef, 20 m - 1 female ov (5.5 mm) slide mount, 3 females (5.5 mm, 5.5 mm, 4.5 mm)+ 1 male, 4 females, 15 im, NCMNB Cat. no. NMCC1991-1204; *Ibid.*, 25 m sand - 3 males, 36 females, 15 im, CMN Cat. no. NMCC1991-1203.

Alaska mainland: 30 miles west Cape Rodney, 24 m. dive, P. Slattery coll., 1981 - 6 females, 3 im, CMN Cat. no. NMCC-1991-1211.

Diagnosis. Female (6.0 mm): Head, rostrum short. Pigmented eyes lacking. Antenna 1, segment 2 strongly setose anteriorly; accessory flagellum inserted nearly apically. Antenna 2, peduncular segment 4, postero-distal lobe medium; posterior margin lined with numerous (>40) plumose setae; segment 5 medium broad, widest distally; flagellar segment 1 with postero-distal setal cluster.

Mandible, palp segment 3 with 14-15 posterior marginal comb spines. Maxilla 2, inner plate with distinct facial row of 6-7 plumose setae. Maxilliped, outer plate medium; palp segment 2, inner lobe large, broad, reaching almost to tip of narrowly clavate segment 3.

Coxae 1 & 2. Gnathopod 1, segment 5 relatively short, deep; segment 6 medium, arcuate. Gnathopod 2, hind margin long-setose; segment 5 slender, shallow, distal spines slender.

Peraeopod 3, coxa squarish; segment 4 short, distally broad; segment 5 strongly setose proximally; segment 6

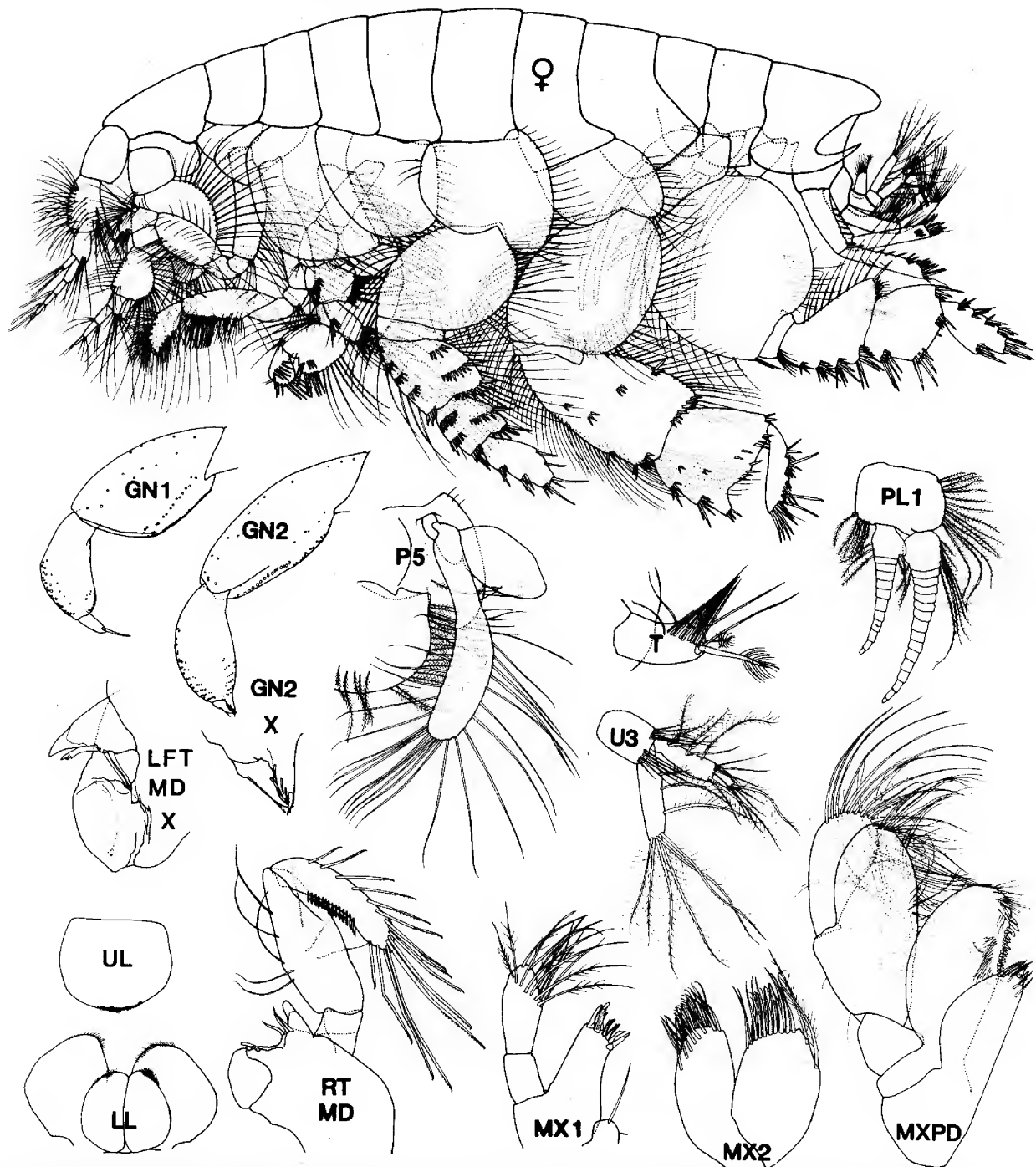


FIG. 1. *Eohaustorius eous*. (Gurjanova). Female ov. (5.0 mm). Bering Sea, Alaska. Slattery coll.

ovate, margins spinose. Peraeopod 4, segment 4 with 23 posterior marginal setae; segment 4 hind lobe short, distally broad, truncate, anterior margin with 1 stout spine group; segment 6 slender, with 21 anterior marginal spine group.

Peraeopod 5, basis broadly ovate, hind margin completely lined with setae; segment 4 short, uniformly broad; facial spine clusters strong; segment 5 medium, not wider than long, facial spine clusters strong; segment 6 broadest medially, anterior margin with 2 spine clusters, posterior margin with 2 single spines. Peraeopod 6, basis medium, hind margin setose throughout; segment 4 elongate, with 3-4 facial spine clusters; segment 5 broadest distally, with 2

weak facial spine groups, 4-5 inner distal and 5-6 outer distal marginal spines; antero-distal emargination medium deep; segment 6 relatively long and slender, with 4-5 clusters of mixed long and short spines. Peraeopod 7, basis broad, hind margin distally narrowing and lined with medium setae; segment 4 slightly wider than long, anterior margin with 3 spine clusters, posterior margin lined with long setae; segment 5 squarish, anterior margin with 1 cluster of long spines; segment 6 little broadened, anterior margin with 1, and posterior margin with 4, clusters of medium spines.

Pleopods, basis stout, broad, outer margin strongly plumose-setose; outer ramus 15-segmented, inner 12-seg-

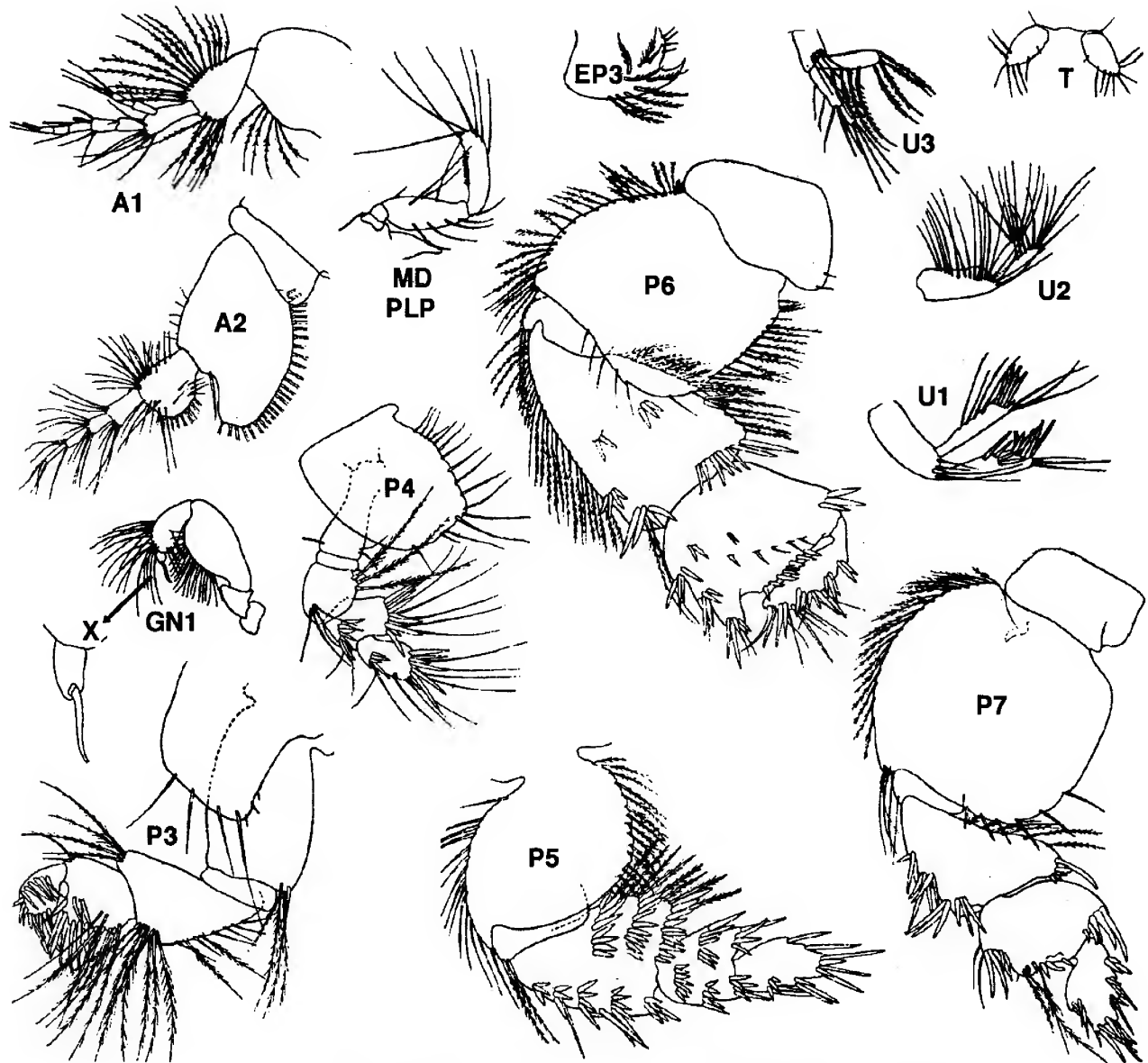


FIG. 2 *Eohaustorius eous* (Gurjanova) Female ov. (6.0 mm). East coast Kamchatka peninsula. (after Gurjanova, 1962)

mented. Pleon plate 3, hind corner strongly produced, nearly straight, acute. Uropod 1, peduncle, outer margin with 4-5 slender spines; inner ramus, posterior margin with short spines. Uropod 3, outer ramus, terminal segment short (<1/2 proximal segment); inner ramus, inner margin with 3 plumose setae.

Telson lobes short, slender, with 12 dorso-distal setae.

Distribution. Eastern Kamchatka & Bering Sea, 20-40 m; western Bering Sea, subtidally to 25 m. Not taken in southeastern Alaska despite apparently suitable habitat (e.g., Glacier Bay) where *E. washingtonianus* was dominant.

Taxonomic commentary. *E. eous* is a relatively primitive species, showing several plesiomorphic character states in common with the N. America estuarine species *E. estuarius*. It is not closely related to *E. robustus*, differing in the character states noted in the key and on p. 37. The material

from the northern Sea of Okhotsk, illustrated in Gurjanova (loc. cit., fig. 136B2) is here considered a variant on the main theme from the Kamchatka peninsula and Bering Searegions.

Eohaustorius estuarius Bosworth
(Figs. 4)

Eohaustorius estuarius Bosworth, 1973: 253, fig. 2 im.—Staupe, 1987: 372 (key), 383, fig. 18.11.—Barnard & Karaman, 1991: 363.

Material examined. 10 lots containing 158 specimens: BRITISH COLUMBIA.

Queen Charlotte Islands, ELB Stns., July-Aug., 1957 (~10 specimens at 3 stations, verified by W. Bosworth, 1973): H8a (Delkatla Slough) - 3 females; H10 (New Masset) - 1 female; W1 (north end Lepas Bay) - 8 males 12 females, 6 im. Vancouver I., north end, ELB Stns., 1959: O12, Ahous Bay,

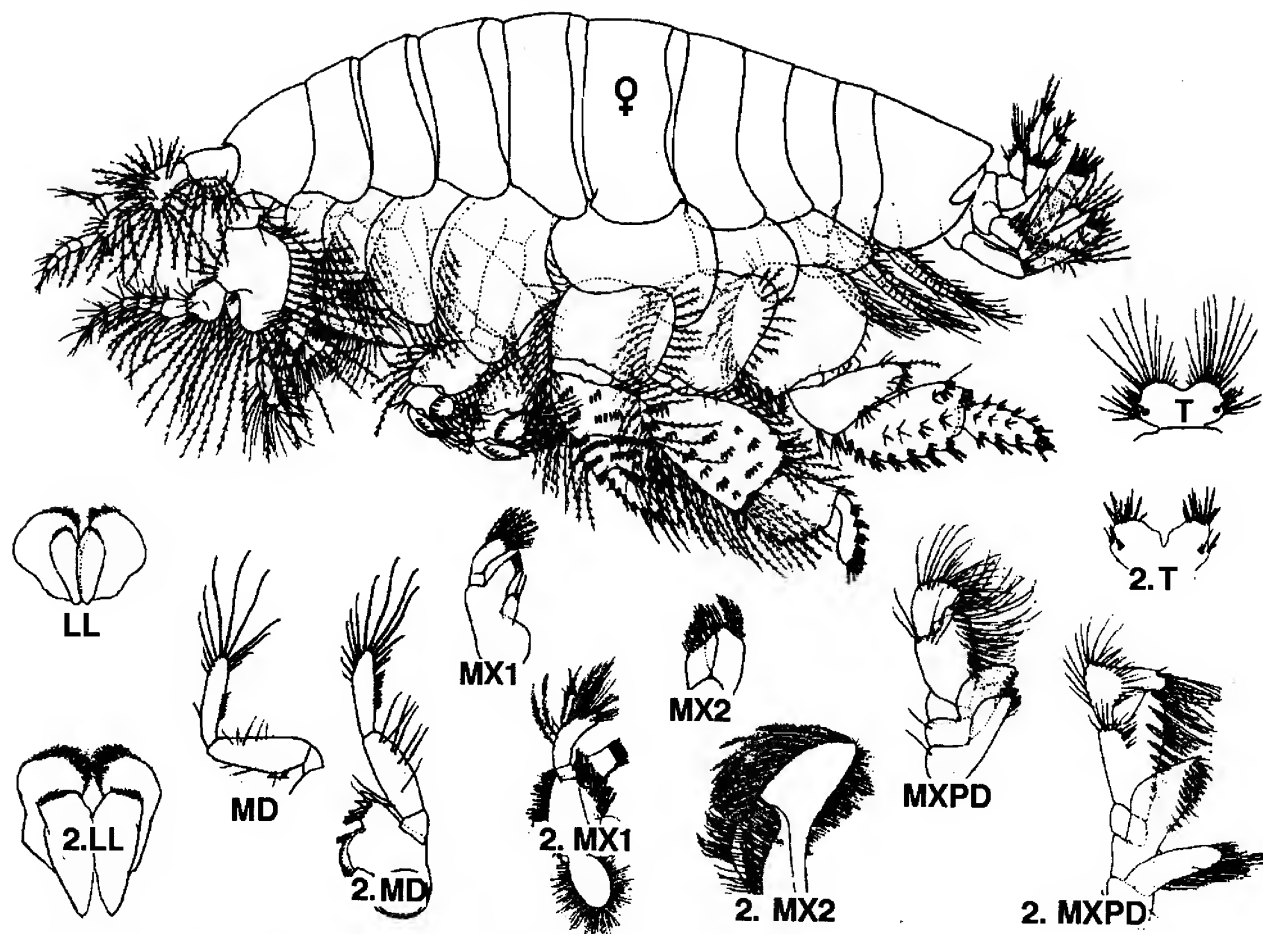


FIG. 3. *Pseudohaustorius caroliniensis* Bousfield. Female (7.6 mm), lateral view; mouthparts, telson
2. *Haustorius canadensis* Bousfield. Female (12.0 mm), mouthparts, telson. (after Bousfield, 1973).

Vargas I. - 3 males, 1 fem, 1 im; Stn. O13, Yarksis, Vargas I. - 4 males, 5 females, 1 im.

Central Vancouver I., ELB Stns., 1955: P1, Clayoquot I. - 1 female, 1 im; P6a, southeast end Wickaninnish Bay - 11 males, 26 females. ELB Stns., July, 1970: P701, south end Long Beach, in surf-exposed sand at freshwater beach seep, LW level - 1 female ov. (5.0 mm), (slide mount) (fig'd specimen), + 17 males, 33 females, CMN Cat. no. NMCC1991-1229; P708, Pachena Bay, mouth of estuary - numerous specimens.

WASHINGTON, OREGON.

ELB Stn. W34, Crescent Beach, east end, near creek mouth - 1 female (4.8 mm), slide mount, +12 other females, 5 males, CMN Cat. no. NMCC-1992-1255; Stn. W41, Sooes estuary, near mouth, in steep sand banks - 1 im.

Diagnosis. Female (5.0 mm): Head, rostrum medium; eyes small, weakly pigmented. Antenna 1, peduncle 2, anterior margin setose nearly to base. Antenna 2, peduncular segment 4, postero-distal lobe large, posterior margin with 25+ plumose setae; segment 5 distally broadest; flagellar segment 1 with distal plumose seta.

Mandible, palp segment 3, inner (posterior) margin with

10-12 marginal comb spines, outer margin with 5-6 mediums etae. Maxilla 2, inner plate with strong facial row of setae. Maxilliped, inner plate tall, slender; outer plate broad, distally truncate; palp segment 2, inner lobe long narrow, reaching tip of broadly expanded palp segment 3.

Gnathopod 1, basis, anterior margin weakly setose throughout; carpus short, deep; dactyl, nail long. Gnathopod 2, carpus relatively short and deep, with sub-apical postero-distal cluster of slender spines.

Peraeopod 3, coxae expanded anteriorly, basis with antero-distal cluster of setae. Peraeopod 4, segment 4 with 2 posterior marginal plumose setae; segment 5, hind lobe medium, proximal margin with a few setae, anterior margin with strong oblique spine row, hind margin truncate, spinose; segment 6 medium, little broadened distally, with single oblique anterior marginal spine group.

Peraeopod 5, coxal hind margin strongly setose; basis medium, hind margin proximally setose; segment 4 relatively short, broad, facial spine groups strong; segment 5 shorter than broad, facial spines strong; segment 6 broadest medially, with 2 anterior marginal spine groups, hind margin with single spine cluster. Peraeopod 6, basis medium, hind margin distally bare; segment 4 relatively short, broadest distally, with 4 weak facial groups of spines; segment 5

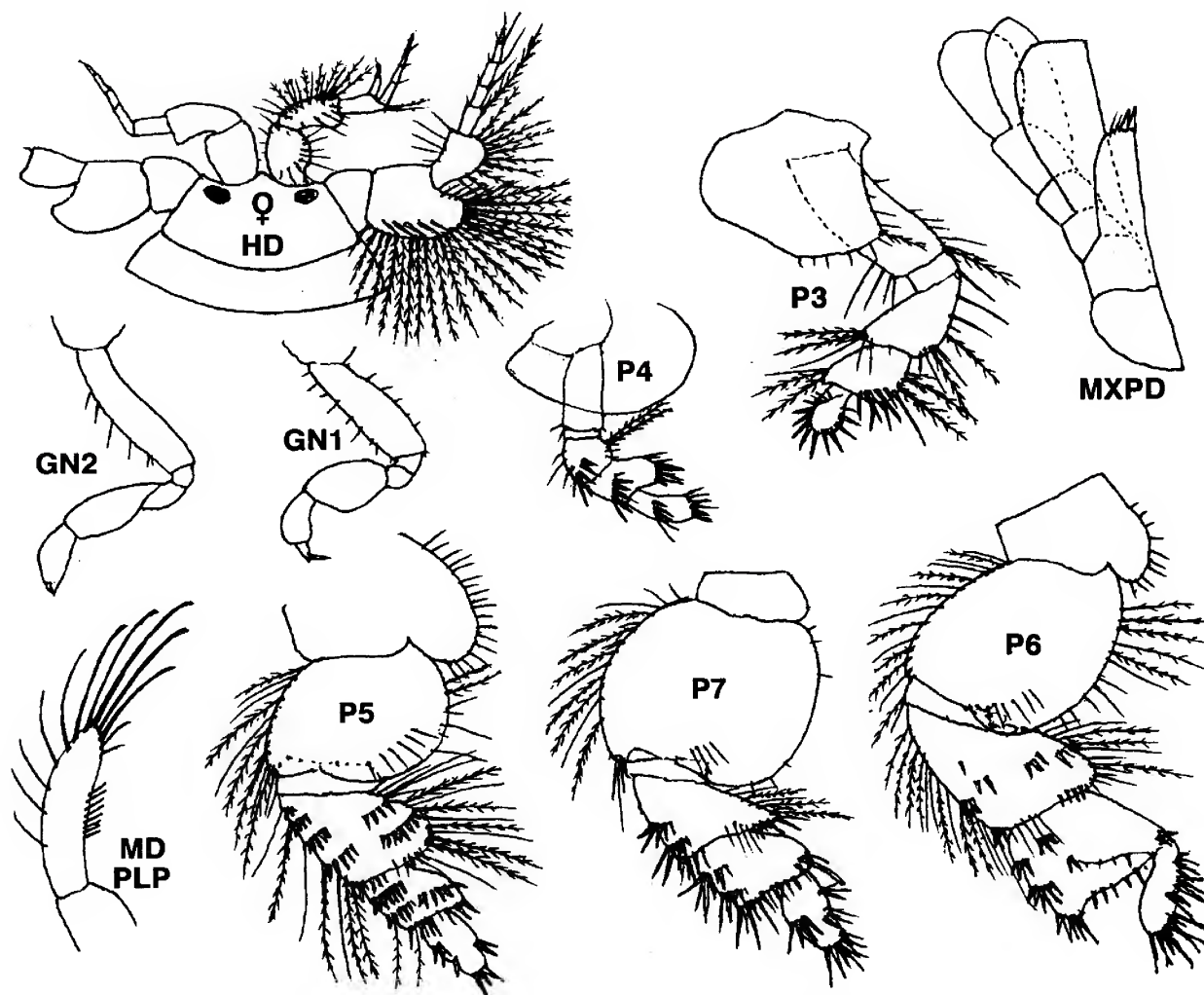


FIG. 4. *Eohaustorius estuarius* Bosworth, Female ov (5.0 mm) Long Beach, V. I., B. C. (partly after Bosworth, 1973)

broader than deep, with 2 small facial clusters of spines, 3-4 spines along inner distal margin, and 9-10 spines along outer distal margin; segment 6 with 6-7 posterior marginal clusters of short and long spines. Peraeopod 7, basis broadly expanded, lacking proximal basal cusp, hind margin nearly bare; segment 4 short, very broad distally, anterior margin with 2 spine clusters, posterior margin lined with plumose setae throughout; segment 5 short, broader than deep, with 2 anterior marginal spine clusters; segment 6 broad, anterior margin strongly convex with single cluster of strong spines, posterior margin with 2 spine clusters.

Pleopods normal for the genus. Pleon plate 3, hind corner strongly produced, straight, acute. Uropod 3 rami relatively short, <2X peduncle; outer ramus medium; inner ramus with few inner marginal seta.

Telson lobes medium broad, regularly setose.

Distribution. Common in freshwater intertidal seeps and rills over open and/or protected sand beaches, from Central California north through Oregon, Washington, and British Columbia to Dixon Entrance; not yet taken in south-eastern Alaska.

Taxonomic commentary. As noted elsewhere (p. 59), this species shows mainly plesiomorphic character states. It is a member of the *E. eous* subgroup and similar to *E. gurjanovae* of the Asiatic North Pacific region..

Eohaustorius subuliculus Hirayama
(Fig. 5)

Eohaustorius subulicola Hirayama, 1985: 43, figs. 155-157.
Eohaustorius subuliculus Barnard & Karaman, 1991: 463.—
Ishimaru, 1994: 64.

Diagnosis. Male (2.25 mm): Head, rostrum short, decurved. Pigmented eyes lacking. Antenna 1, accessory flagellum medially inserted on peduncular segment 3. Antenna 2, peduncular segment 4, antero-distal lobe shallow; hind margin with few (~17) plumose setae; segment 5 of medium width; flagellar segment 1 with single large postero-distal seta.

Mandibular palp, segment 3 with few (4-5) comb spines. Maxilla 1, outer plate with 8 apical spines. Maxilla 2, inner plate with 6-7 submarginal facial row of setae. Maxilliped,

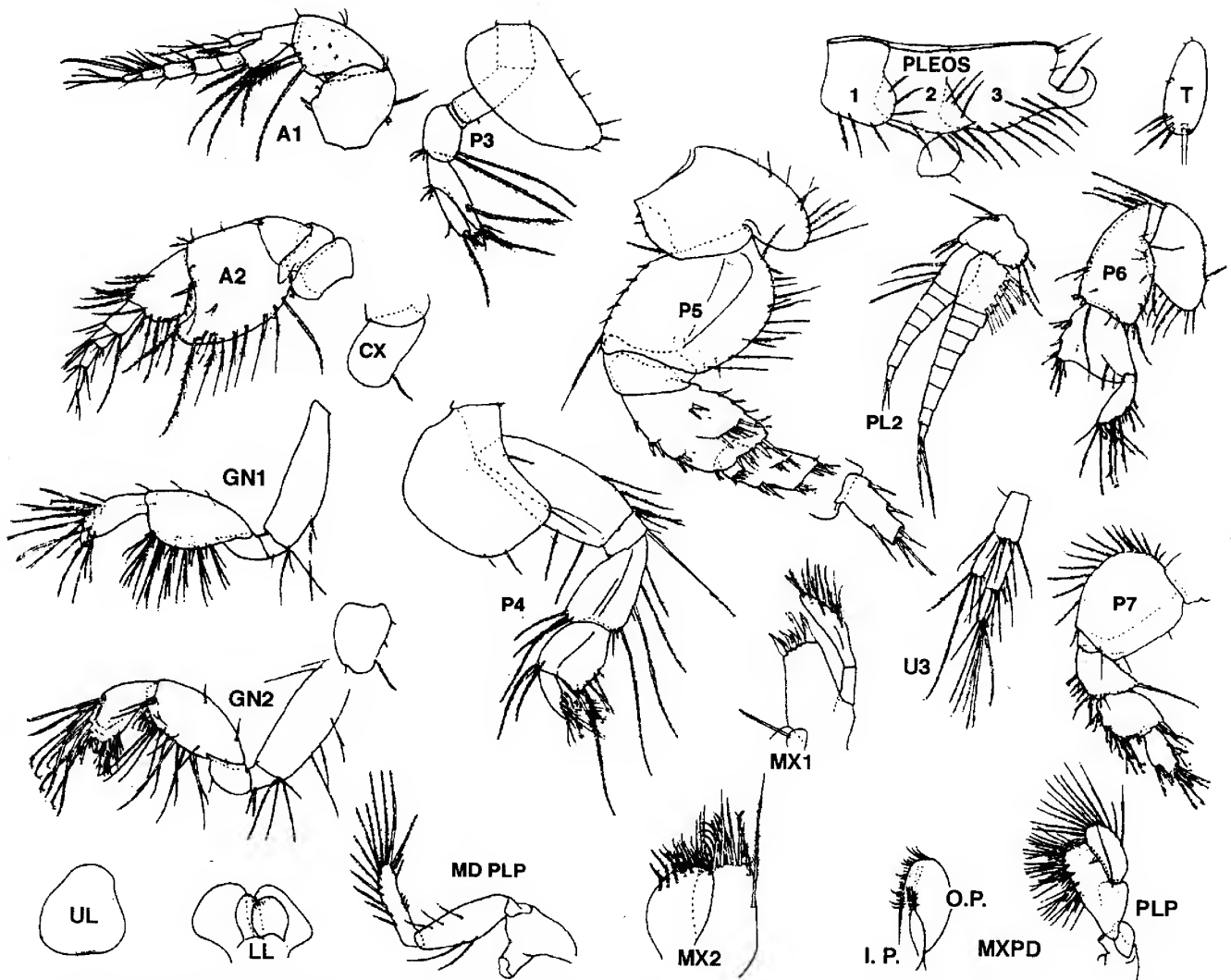


FIG. 5. *Eohaustorius subuliculus* Hirayama. Male (2.25 mm). Tomioka Bay. (after Hirayama, 1985).

palp segment 3 narrowly clavate; outer plate narrow.

Coxa 1 vestigial; coxa 2 small rounded below, hind margin with single seta. Gnathopod 1, segment 5 short and deep; segment 5 slender. Gnathopod 2, basis with ~5 hind marginal setae; segment 5 with 5 distally spoon-shaped spines.

Peraeopod 3, basis, hind margin with distal setae only; segment 5, hind margin lacking proximal setae; segment 6 narrow. Peraeopod 4, coxa slender smoothly convex in front; basis hind margin bare; segment 4 with 4 posterior marginal setae; segment 5 (carpus), posterior lobe slender acute, lacking spines; segment 6 slender, with apical spine(s) only.

Peraeopod 5, basis, posterior margin setose throughout; segment 4 narrow, longer than broad, facial spines medium; segment 5 slender; segment 6 slender, with single anterior marginal spine. Peraeopod 6, basis, hind margin setose throughout; segment 4 little broadened, facial spines lacking; segment 5 broadest distally, lacking facial spines, distal margin with a few spines near hinge; segment 6, postero-distally with slender split-tipped spines and long setae. Peraeopod 7, basis lacking proximal cusp, hind margin straight,

nearly bare; segment 4 slender, hind margin nearly bare; segment 5 as long as broad, anterior margin with 3-4 slender spine groups; segment 6 slender with single anterior marginal spine cluster and elongate pectinate apical spines.

Pleopods, peduncle small; rami slender, outer ramus 9-10-segmented. Pleon plate 3, hind corner strongly produced, hooklike, extending well beyond postero-dorsal process. Uropod 1, rami with apical spines and setae. Uropod 3, rami slender; inner ramus lacking inner marginal setae; outer ramus, terminal segment strong ($> 2/3$ inner segment).

Telson lobes slender, marginal setae few.

Distribution. Tomioka Bay, Japan; subtidal.

Taxonomic commentary. *Eohaustorius subuliculus* is distinctive on the basis of reduction of some character states, and special development of others. Hirayama (1985) described the species from the type male and four additional specimens. He noted its general resemblance to *E. cheliferus*, but *E. subuliculus* may qualify for separate subgeneric status.

Eohaustorius sawyeri, Bosworth
(Fig. 6)

Eohaustorius sawyeri Bosworth, 1973: 257, fig. 1a-e.—Austin, 1985: 607.—Staude, 1987: 383, 372 (key).—Barnard & Karaman, 1991: 363.

Material examined. Six lots containing 37 specimens (both sexes and subadults), from 4 localities in British Columbia, and two in California:
BRITISH COLUMBIA.

Vancouver I., southern end: Off Long Beach, V. I., 22 m, P. Slattery Stn., 1982 - 3 males, CMN Cat. no. NMCC1991-1219. ELB Stn. P21a, Trevor Channel, off Bordelais I., 44 m, fine sand, Aug. 9, 1975 - 1 female (3.2 mm) (slide mount) (**figured specimen**), CMN Cat. no. NMCC1991-1227; *Ibid.*, Stn. B9c, off Second beach, 20-25 m, medium sand, June 28, 1976 - 1 female; ELB Stn. H41, Jordan R., black silty sand, LW, July 27, 1964 - female ov (5.2 mm).

CALIFORNIA

Off Marine Laboratory, Moss Landing, 2 m sand, P. Slattery coll., June 1, 1982 - 2 males, 7 females, CMN Cat. no. NMCC1991-1240; *Ibid.*, 12 m, July 1, 1982 - 5 males, 8 females, CMN Cat. no. NMC1991-1239.

Diagnosis. Female im. (3.2 mm.): Head, rostrum. Eyes whitish, not pigmented. Antenna 1, peduncle 2, anterior margin weakly setose, singly inserted. Antenna 2, peduncle 4, postero-distal lobe medium, posterior margin with 30+ plumose setae, antero-distal lobe strong, extending >2/3 length of segment 5; segment 5 relatively shallow; basal flagellar segment with 3-4 distal plumose seta.

Mandible, palp segment 3 with 8-11 posterior marginal comb spines. Maxilla 1, palp stout, proximal segment short (<1/2 segment 2). Maxilla 2, inner plate, facial setae submarginal. Maxilliped, outer plate medium; palp segment 2, inner lobe narrow, shorter than medium-large segment 3.

Gnathopod 1, coxa subquadrate; basis broadened medially, anterior margin smooth distally; segment 5 elongate, medium deep; segment 6, thick (deep). Gnathopod 2, basis, anterior margin smooth; segment 5 slender, lower margin straight.

Peraeopod 3, coxa 3 subquadrate; segment 4 short, very broad distally; segment 5 deep, with antero-proximal invagination, hind margin proximally setose; segment 6 large, lozenge-shaped, margins slender-spinose. Peraeopod 4, segment 4 with 4 postero-marginal setae; anterior margin with distal spine group; segment 5, anterior margin with fan-wise spine row, hind lobe short, postero-proximal margin with 2 spine clusters; segment 6 stout, broadening distally, with 2 anterior and 2 posterior marginal spine clusters.

Peraeopod 5, basis broadly ovate, hind margin nearly bare distally; segment 4 short, strongly broadest distally, facial spines strong; segment 5 expanding distally, longer than broad, facial spines strong; segment 6 broad, apex truncate, anterior margin with 1, posterior margin with 3

spine clusters. Peraeopod 6, basis medium broad, hind margin lightly setose proximally; segment 4 long, broadest distally, with several strong facial spine clusters; segment 5 broadening distally, with 2 strong facial spine clusters antero-distal margin with 12-15 spines, excavation shallow; segment 6 slender, with 4-5 posterior marginal spine clusters. Peraeopod 7, posterior margin of coxa broadly acute; basis broad, convex hind margin distally with a few short setae, lacking proximal cusp; segment 4 short, broadest distally, hind margin setose; segment 5 broader than deep, anterior margin with single spine group, antero-distal free margin broad, lined with spines, postero-distal angle with long heavy spine; segment 6 broad, anterior margin with 1, posterior margin with 3-4 stout spine groups.

Pleopods, peduncle short broad, outer margin strongly plumose-setose; outer ramus 16-segmented, inner ramus 13-segmented. Pleon plate 3, hind corner moderately produced, acute, strongly overhung by, and much shorter than, postero-dorsal process of pleosome 3. Uropod 1, peduncle, outer margin with 3-4 slender spines, distal spine cluster medium; inner ramus posteriorly setose; outer ramus narrow, apex sub-acute. Uropod 3, outer ramus slightly the longer, terminal segment medium; inner ramus lacking inner marginal setae. Telson lobes short, broad, with few dorso-distal setae.

Distribution. A southern species, abundant along coasts of California and Oregon, diminishing in Washington, and barely entering British Columbia. Occurs along outer surf-exposed sand beaches, from MLW to shallow subtidally.

Taxonomic Commentary. The large female specimen from Jordan R. exhibited a very broad segment 6, and heavy facial spines on segments 4 & 5 of peraeopods 5 and 6.

Eohaustorius sencillus J. L. Barnard
(Fig. 7)

Eohaustorius sencillus Barnard, 1962: 249, figs 1, 2.—Bosworth, 1973: 8 (key).—Barnard, 1975, fig. 44.—Barnard & Karaman, 1991: 363.

Material examined. Mile buoy, off Moss Landing, California, 20 m sand, P. Slattery coll., Feb. 24, 1971 - 1 female (slide mount) (**figured specimen**), CMN Cat. no. NMCC1991-1241; 13 additional females, 2 males.

Diagnosis. Female (3.5 mm): Head, rostrum short. Pigmented eyes lacking. Antenna 1, peduncular segment 2, anterior margin weakly setose, bare proximally. Antenna 2, peduncular segment 4 relatively short and deep, postero-distal lobe medium, hind margin with 25-30 plumose setae; segment 5 as deep as long; basal flagellar segment postero-distally with 4-5 long setae.

Mandible, palp segment 3 slender, with 7 posterior marginal comb spines. Maxillae undescribed. Maxilliped, outer plate broad; palp segment 2, medial lobe large, broad, shorter than moderately broadened terminal segment.

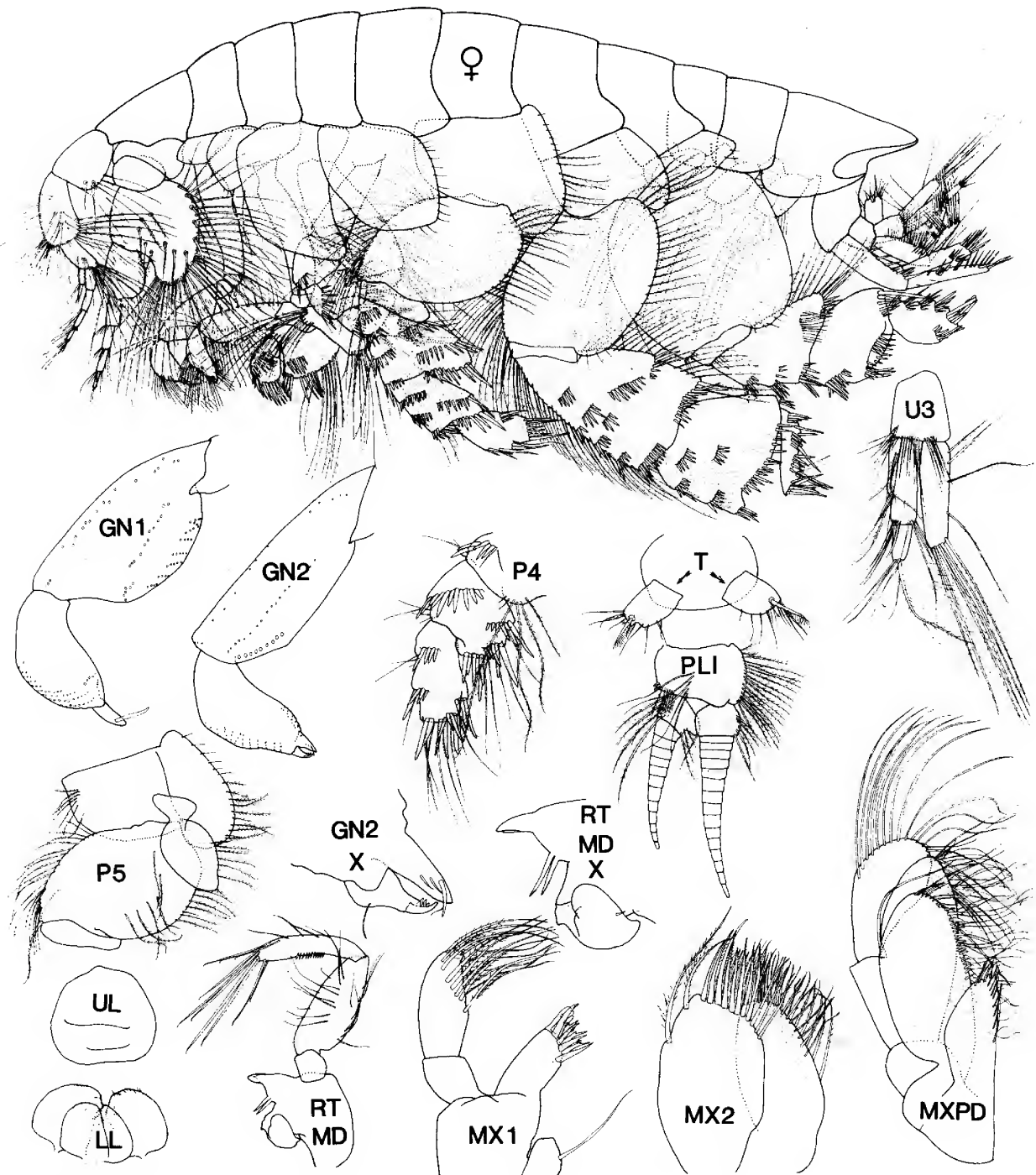


FIG. 6. *Eohaustorius sawyeri* Bosworth, 1973. Female ov (3.2 mm). Off Long Beach, V.I., B.C.

Coxae 1 & 2 squarish below. Gnathopod 1, basis with 7-8 posterior marginal setae; segment 5 medium, deep, convex below; segment 6 sharply broadest medially; dactyl, unguis large, heavy. Gnathopod 2, basis lined posteriorly with longish setae; segment 5 slender, strongly setose; postero-distal spines few, weak; segment 6 slender, regular.

Pereopod 3, coxa deep, sublunate; segment 4 medium broad distally, hind margin with 7-9 setae; segment 5 relatively shallow, anterior margin bare, not emarginate proximally, lower margin proximally setose; segment 6 lenticular,

margins slender spinose. Pereopod 4, segment 4 relatively large, hind margin convex, with 2-3 long setae, anterior margin with weak oblique spine row; segment 5, with weak anterior oblique spine row, posterior lobe medium, rounded behind, with 2 weak postero-proximal spine groups; segment 6 slender, with anterior marginal spine cluster, and 2 postero-distal single marginal spines.

Pereopod 5, basis ovate, hind margin lacking distal setae; segment 4 not broader than deep, parallel-sided, facial spine groups weak; segment 4 relatively small, not wider

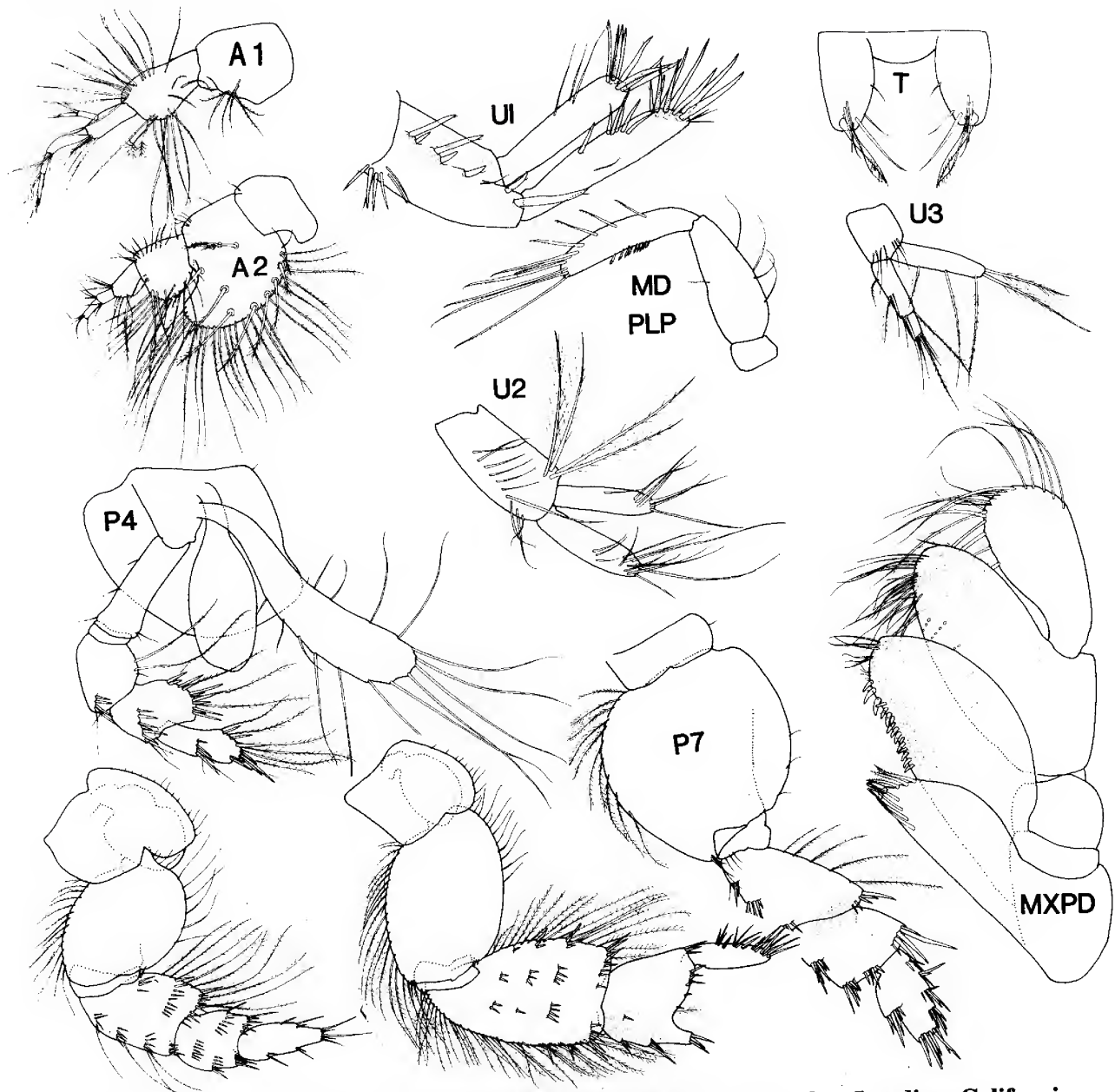


FIG. 7. *Eohaustorius sencillus* Barnard, 1962. Female (3.5 mm). Off Moss Landing, California.

than deep, facial spine groups weak; segment 6 not broadened, anterior and posterior margins each with 2 single slender spines, apex narrowly truncate, weakly spinose. Peraeopod 6, coxa narrow, deep; basis relatively little broadened, hind margin with proximal setae only; segment 4 elongate, broadest medially, with 6 small facial spine clusters; segment 5 not broader than deep, with single facial spine; antero-distal margin with 4-5 spines, excavation deep; segment 6 regular, hind margin with 4-5 clusters of slender spines. Peraeopod 7, basis large, medium broad, subovate, hind margin virtually bare, lacking proximal cusp; segment 4 longer than broad, gently broadening distally, anterior margin with 2 spine clusters, hind margin with 5 plumose setae; segment 6 slightly broader than deep, with anterior spine cluster; anterior distal free margin relatively short; segment 6 medium broad, anterior margin with 1, posterior margin with 3-4 spine clusters, apex truncate, spinose.

Pleon plate 3, hind corner acutely produced, short, tip directly beneath dorsal hind process. Uropod 1, peduncle, outer margin nearly bare, distal spine cluster weak; inner ramus weakly setose posteriorly; outer ramus, posterior margin with slender spines. Uropod 3, rami subequal, length ~2X peduncle; outer ramus, terminal segment very short (<1/3 proximal segment); inner ramus, hind margin nearly bare. Telson lobes short, broad, with 6-8 dorso-distal setae.

Distribution. From Pt. Conception north through California to Southern Oregon (Bosworth), subtidally to 20 m; not reaching Canadian waters.

Taxonomic Commentary. This species is distinguished by the relatively large basis of peraeopod 7, and large dactyl of gnathopod 1. Bosworth (pers. communic.) recognized a variant in deeper water material of J. L. Barnard (loc. cit.).

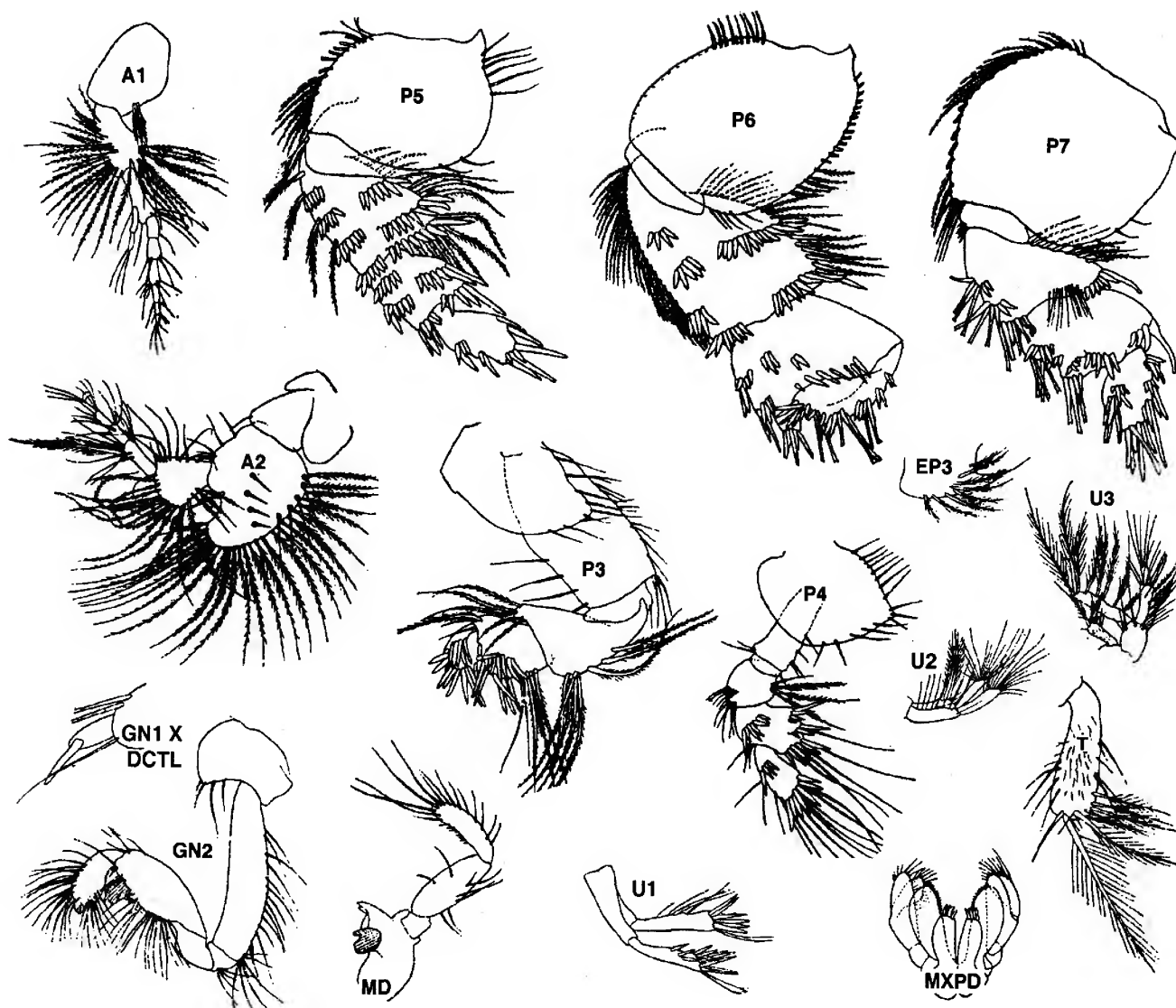


FIG. 8. *Eohaustorius gurjanovae*, new species. Female ov (6.0 mm). Southern Sakhalin I., Sea of Japan. (modified from Gurjanova, 1962)

Eohaustorius gurjanovae, new species
(Fig. 8)

Eohaustorius washingtonianus Gurjanova, 1962: 404, figs. 135B, V.

Type material. Female ov (6.0 mm), **Holotype**; 7 females and males, **Paratypes**, from south coast of Sakhalin I., Sea of Japan; collections of the Zoological Museum, St. Petersburg, Russia.

Diagnosis. Female (7.0 mm): Head, rostrum short; pigmented eyes lacking. Antenna 1, peduncle 2 anteriorly setose throughout. Antenna 2, peduncular segment 4, posterior margin with 25-30 plumose setae; postero-distal lobe large, extending to mid-point of deep segment 5; basal flagellar segment with 1 stout postero-distal plumose seta.

Mandibular palp medium, with 7-8 posterior marginal

comb-spines. Maxillae 1 & 2 undescribed. Maxilliped, outer plate slender, tall; palp segment 2, inner lobe slender, long, nearly reaching tip of clavate palp segment 3.

Gnathopod 1, coxa, hind corner squarish; dactyl, body palm-shaped, unguis large. Gnathopod 2, basis, posterior margin lined with medium setae; segment 5 slender, postero-distal spine cluster strong; segment 6 much shorter, slender.

Peraeopod 3, coxa, anterior margin rounded; basis thick, heavy; segment 4 short, expanding to broad distal margin, antero-distal angle and posterior margin with several plumose setae. Peraeopod 4, coxa subquadrate, lower and hind margins setose; basis with a few postero-distal setae; segment 4, hind margin with 3-4 plumose setae, anterior margin with medial cluster of slender spines; segment 5 hind lobe short, anterior margin with oblique row of stout spines, postero-proximal margin with 2 groups of stout spines; segment 6 short, broadening distally to large apical cluster of spines, anterior margin with single spine cluster and a few setae.

Peraeopod 5, basis broad, orbicular, hind margin devoid of setae except proximally and mid-distally; segment 4 broadening gradually, longer than wide, with clusters of stout facial spines; segment 5 smaller and narrower, facial spines strong; segment 6 broad, anterior margin with 2 clusters of stout spines, posterior margin with 2 singly inserted spines, apical spines strong. Peraeopod 6, basis medium broad, hind margin setose throughout, except for short distal gap; segment 4 short, very broad, with 2 anterior clusters and 1 posterior submarginal row of stout spines; segment 5 much broader than deep, with 2 facial spine clusters, and 6-7 antero-distal marginal spines, distal excavation medium deep; segment 6 large, bent forward, hind margin with 6 clusters of spines, some elongate distally. Peraeopod 7, basis very broad, hind margin with 4-5 medio-distal setae and blunt proximal cusp; segment 4 broadly triangular, anterior margin with 2 spine clusters, hind margin setose throughout; segment 5 large, slightly broader than segment 4, anterior margin with 2 spine clusters, antero-distal free margin heavily spinose, postero-distally angle with medium stout spine; segment 6 medium, anterior margin with 3-4, and posterior margin with 3, spine clusters, some spines elongate, apex broad, heavily spinose. Long anterior marginal spines are split-tipped or clavate.

Pleon plate 3, hind corner normally produced, acute, not elongate, with several lower marginal and submarginal plumose setae. Uropod 1, peduncle, outer margin weakly or not spinose; outer ramus, posterior margin with subapical fan of spines; inner ramus, posterior margin distally with long setae. Uropod 2, peduncle and rami regularly setose. Uropod 3, rami subequal, shorter than 2X peduncle; terminal segment of outer ramus short; inner ramus with 4-5 inner marginal setae. Telson lobes slender, each with 5-6 dorso-distal plumose setae and several inner marginal fine setae.

Etymology. The species is named in honour of the late Eupraxie F. Gurjanova who first recorded and figured the material from the Soviet far eastern region, as reproduced here.

Distribution. South coast of southern Sakhalin I., Sea of Japan, in sand at 19 m. depth.

Taxonomic commentary. *E. gurjanovae* is another member of the advanced group of species including *E. robustus*, *E. cheliferus* and *E. washingtonianus*. As noted by Dr Gurjanova (loc. cit., p. 405), this species differs from the North American Pacific species, *E. washingtonianus*, in a number of morphological character states, including the stronger armature of peraeopods 5-7, the more numerous carpal spines of gnathopod 2, and the linear setose lobes of the telson. Together these two forms do not qualify as a pan-Pacific sibling species pair and are here considered distinctly separate species.

***Eohaustorius robustus* (Gurjanova) new status**
(Fig. 9)

Haustorius eous robustus Gurjanova, 1953:216.

Eohaustorius robustus eous Gurjanova, 1962:409.—Barnard & Karaman: 363.

Material examined. No specimens were taken in the North American study region.

Diagnosis. Female (6.5 mm): Head, rostrum short. Pigmented eyes lacking. Antenna 1, flagellum short, peduncular segment 2 with thick, coarse, facial plumose seta distally. Antenna 2, peduncular segment 4 short and deep, hind margin with ~35 plumose setae; postero-distal lobe large; segment 5 deepest mid-distally; basal flagellar segment postero-distally with 3 short plumose setae.

Mandibular palp, segment 3 relatively broad, shorter than 2 relatively, with 7 posterior marginal comb spines. Maxillae and maxillipeds not described or figured.

Coxae 1 & 2 small, regular. Gnathopod 1, basis, hind margin sparsely setose; segment 5 large, deep, strongly setose behind; segment 6 short broad; dactyl with long straight unguis. Gnathopod 2, basis, hind margin with several long setae; segment 5 elongate, postero-distal spines numerous, short, apically spoon-shaped; segment 6 short, apically narrowing abruptly.

Peraeopod 3, coxa rectangular, basis, hind margin setose throughout; segment 4 broadening gently distally, hind margin setose throughout; segment 5, anterior margin with proximal excavation or notch, hind margin proximally with plumose setae; segment 6 lenticular, marginal spines strong. Peraeopod 4, coxa rounded anteriorly, with squared hind corner; basis with antero- and postero-distal clusters of setae; segment 4, hind margin with 5 setae, 3 longish; segment 5, anterior margin with single setal cluster, hind lobe medium, antero-distal spine cluster strong, distal margin bare; segment 6 small, short, with hind margin and apical spine clusters.

Peraeopod 5, coxa deep, hind margin strongly setose; basis asymmetrically broad, hind margin distally bare; segment 4 broadening distally, with strong marginal and facial spine clusters, and strong postero-distal setal cluster; segment 5 narrower, squarish, with stout spine clusters; segment 6 medium, with 1 anterior marginal spine cluster, and a few posterior marginal and apical spines. Peraeopod 6, basis relatively short and very broad, broadest distally, hind margin short-setose; basis large, broadening distally, with strong anterior facial clusters and posterior facial row of spines; segment 5 broadest distally with 2 strong anterior facial spine clusters; antero-distal margin with 9-10 spines, excavation deep; segment 6 large, bent forward, hind margin with 5 spine clusters, some distal spines elongate, tips funnel shaped, notched. Peraeopod 7, basis very broad, proximally truncate

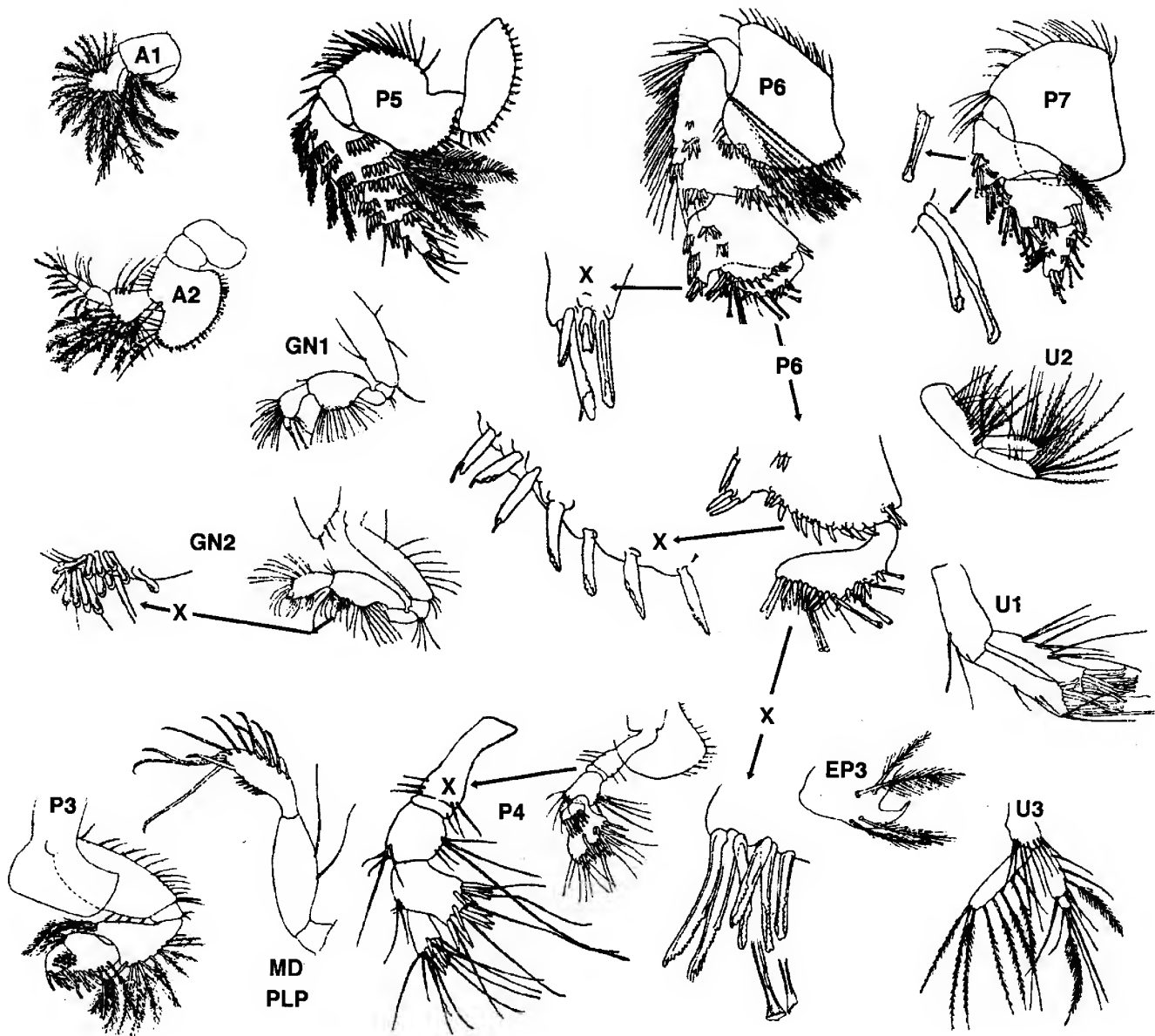


FIG. 9. *Eohaustorius robustus* (Gurjanova). Female (7.0 mm). Greater Kurile Islands. (modified from Gurjanova, 1962).

behind, margin smooth; segment 4 short, very broad, hind lobe narrow, with apical cluster of plumose setae; segment 6 short, very broad, with 2-3 anterior marginal, and 3 posterior marginal spine groups. Longest anterior marginal spines of segments 4-6 are club- or funnel-tipped.

Pleon side plate 3 with a few facial and submarginal plumose setae; hind corner moderately produced, acute, apex upturned slightly. Uropod 1, rami and peduncle subequal, both rami with distally hooked apical spines; outer ramus with weak subapical setae, inner ramus, posterior margin with 3 groups of long setae. Uropod 2 rami shorter than peduncle, normally setose. Uropod 3, rami short, less than 2X peduncle; terminal segment of outer ramus very short (1/4 proximal segment); inner ramus, inner margin with 5-6 stout plumose setae.

Telson lobes medium, narrowing distally, with about 7 dorso-distal setae.

Distribution. Pacific coast of the Large Kurile Island chain (Paramushir, Iterup Islands), and sublittoral of the northwestern Sea of Okhotsk, at depths of 10-40 m.

Taxonomic commentary. Another species of the advanced subgroup (including *E. cheliferus*), but distinguished by characters given in the key (p. 37). It is not at all closely related to *E. eous*, from which it is distinguished by a combination of 3-4 species level character states. *E. robustus* is superficially close to *E. gurjanovae* in several character states of pereopods 5-7.

Eohaustorius brevicuspis, Bosworth
(Fig. 10)

Eohaustorius brevicuspis Bosworth, 1973: 255, figs. 1-3.
—Austin, 1985: 605.—Stade, 1987: 383, 372 (key).—
Barnard & Karaman, 1991: 363.

Material examined. 4 lots containing 20 specimens,
none from British Columbia.

WASHINGTON.

ELB Stn W39, Neah Bay, Clallam Co., medium sand at LW,
July 30, 1966 - 3 males, 2 females, 1 im. NMCC1991-1233;
ELB Stn. W46, Leadbetter Pt., Pacific Co., surf exposed sand
at LW, Aug. 4, 1966 - 4 males, 2 females, NMCC1991-1236.

OREGON.

ELB Stn. W58, Seal Rock, Lincoln Co., LW surf sand, Aug.
13, 1966 - 1 female ov (4.5 mm) (slide mount) (**figured
speci-men**), 1 female ov (4.6 mm) slide mount, CMN Cat.
no. NMCC1991-1237; 4 males, 5 imm.

CALIFORNIA.

ELB Stn. C1, Crescent City, surf sand beach at LW - 1
subadult female, NMCC1991-2094.

Diagnosis. Female ov (4.0 mm): Head, rostrum short,
blunt, not exceeding antero-lateral head lobes. Eyes small
ovate, adjacent to anterior margin, whitish, lacking pigment.
Antenna 1, peduncular segment 2 with strong anterior mar-
ginal clusters of setae. Antenna 2, peduncular segment 4
short, medium deep, hind margin with relatively few (18-20)
plumose setae, postero-distal lobe short; segment 5 little
broadened distally.

Mandible, palp segment 3 medium long, with 12 poste-
rior marginal comb spines. Maxilla 1 & 2?? Maxilliped,
outer plate medium; palp segment 2, inner lobe relatively
small, distinctly exceeded by broadly expanded palp seg-
ment 3.

Coxa 1?, coxa 2 rounded below. Gnathopod 1, basis,
anterior margin proximally with short setae, posterior mar-
gin distally with a few long setae; segment 5 long, deep;
segment 6 short, distally slightly broadening. Gnathopod 2,
basis, anterior margin medially setose, posterior margin with
a few longish setae; segment 4 slender, shallow; segment 6
short, not medially broadened.

Peraeopod 3, basis, anterior and posterior margins distally
with a few long setae; basis medium broad distally, hind
margin sparsely plumose-setose, segment 5 shallow, with
postero-proximal marginal setae; segment 6 small, lenticu-
lar, margins spinose. Peraeopod 4, coxa very broad, lower
margin nearly straight; segment 4, anterior margin with 2
small groups of setae, hind margin with pair of long plumose
setae; segment 5, anterior marginal oblique spine row strong,
posterior lobe medium, hind margin proximally with a few
spines and setae, distal margin with weak spine cluster;
segment 6 medium, anterior margin with 2 weak clusters of

spines and setae, hind margin distally to apex with a few
longish setae and medium spines.

Peraeopod 5, coxa shallow, hind lobe, lower margin
setose; basis broader than deep, hind margin setose through-
out; segment 4 slightly broadening distally, anterior clusters
and posterior rows of facial spines strong; segment 5 slightly
narrower, facial spines strong; segment 6 medium, with 2
anterior marginal spine clusters, posterior margin with single
spines. Peraeopod 6, basis broadening distally, with large
postero-distal lobe, hind margin setose proximally; segment
4 very broad distally, with 2 weak facial spine groups;
segment 5 short, very broad with 1 posterior and 2 anterior
submarginal facial spine groups, distal margin with 6-7
spines, distal excavation medium; segment 6, short, thick,
posterior margin with 6-7 spine clusters, long spines split-
tipped. Peraeopod 7, basis very broad, suborbicular, hind
margin nearly bare, with broadly rounded proximal cusp;
segment 4 short very broad distally, anterior margin with 3
spine clusters, posterior margin with a few plumose setae
distally; segment 5 narrower, but wider than long, anterior
margin with 2-3 spine clusters, postero-distal corner with
short to medium spines; segment 6 broad, with 1 anterior and
2 posterior marginal spine clusters and long spines at trun-
cate apex.

Pleon plate 3, hind corner moderately strongly produced,
tip acute, not upturned. Uropod 1, peduncle, outer margin
with a few distal spines and apical cluster of 3 heavy spines;
rami with strong apical spine clusters; inner ramus with
several long posterior marginal setae and a medio-distal
cluster of spines; outer ramus with a few posterior marginal
spines; uropod 3, rami subequal, ~2X peduncle, terminal
segment of outer ramus medium; inner ramus, inner margin
with 3-4 plumose setae.

Telson lobes short, thick, with 7-8 dorsal distal setae and
several inner marginal setae.

Distribution. Central California north to the Strait of
Juan de Fuca, in clean medium sand of surf exposed high
salinity beaches, MW level to immediate subtidal depths.

Taxonomic commentary. *E. brevicuspis* is closely
similar to the intertidal species *washingtonianus*, overlap-
ping it distributionally in the Oregon-Washington region, and
replacing it further south.

Eohaustorius washingtonianus (Thorsteinson)
(Figs. 11, 12)

Haustorius washingtonianus Thorsteinson, 1941: 61, figs.
39-51.

Eohaustorius washingtonianus J.L. Barnard, 1957: 81(part).
—Barnard, 1962: 249 (key).—Bosworth, 1973: 8 (key), fig.
E.—Austin, 1985: 607.—Stade, 1987: 383, 372 (key).—
Barnard & Karaman 1991: 363.

non: *Eohaustorius washingtonianus* Barnard, 1957: Pl. 16.
—Gurjanova, 1962: fig. 135A.

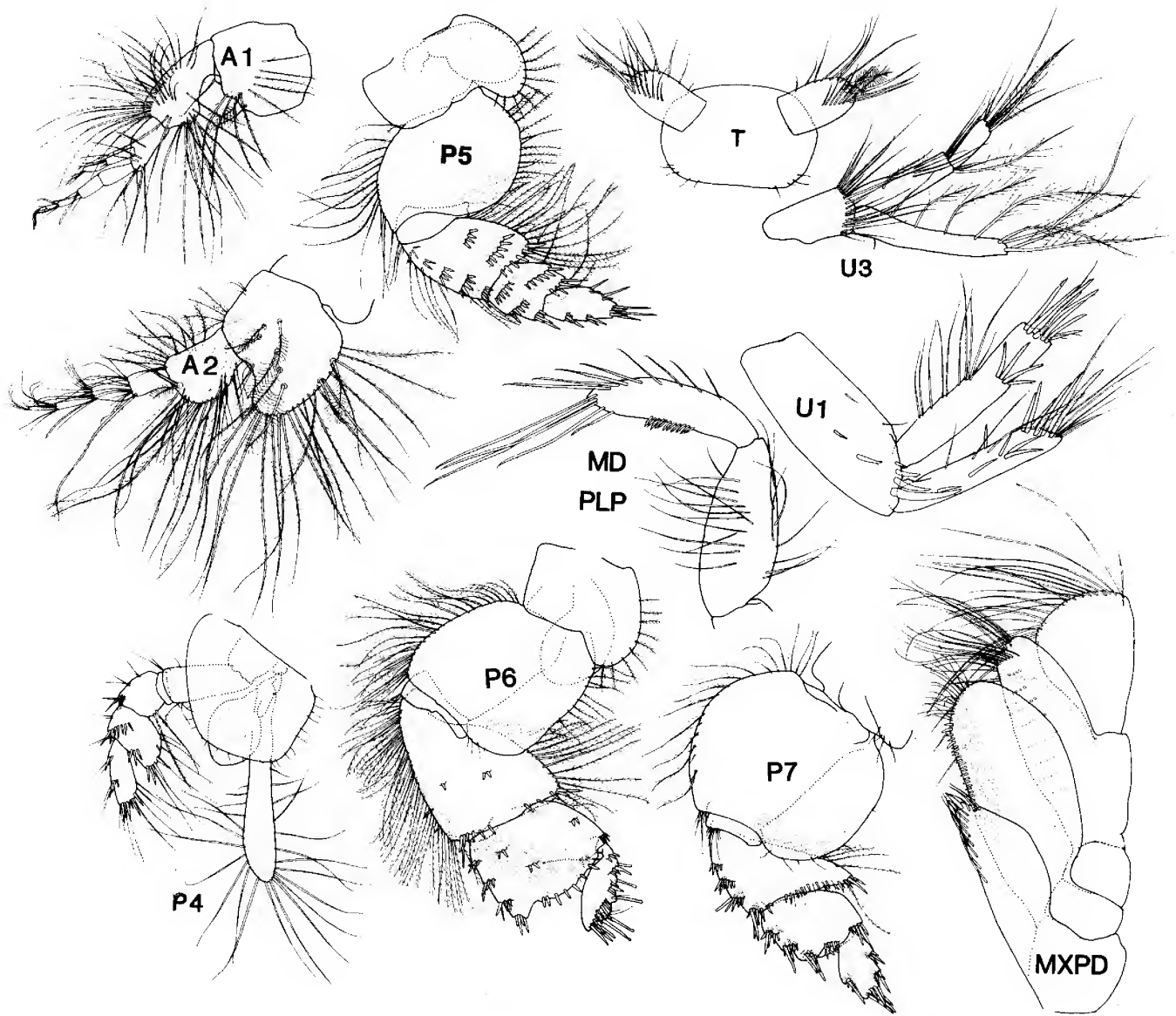


FIG. 10. *Eohaustorius brevicuspis* Bosworth, 1973. Female ov (4.5 mm). Seal Rock, Oregon.

Material examined. About 55 lots containing approx. 600 specimens, of all sexes and life stages (except very juvenile), as follows (numbers of specimens in parentheses):

SOUTHEASTERN ALASKA.

Prince William Sound to Alexander Archipelago, ELB stns., June-Aug., 1961, LW and shallow sub-tidal levels - A54 (3); A71 (1); A81 (30); A83 (1); A121 (1); A140 (1). ELB Stns, July 28 - Aug. 4, 1980: S4B1 (1); S4B2 (f.w. stream outflow) (2); S11B3 (15); S16B1 (1); S16B4 (2); S19B1 (2); S16B4 (2).

BRITISH COLUMBIA.

Queen Charlotte Islands, ELB Stns, July-August, 1957: H3 (1); H8a (2); H13 (29); H14 (17); E1 (12); E14b (31); E17 (4); E21 (1); W2 (44).

North-central mainland coast, ELB Stns, July, 1964: H1 (3); H10 (11); H23 (48); H39 (15); H48 (32); H50 (49); H59 (3).

Northern Vancouver I. & adjacent mainland: ELB Stns, 1959: N1 (15); N6 (16); O13 (1).

Central Vancouver I., ELB Stns 1975: P28 (48); P29 (1). Southern Vancouver I., ELB Stns., 1955: F4, Albert Head, near Victoria (2); F5 (9); P6a (8); P8 (4). ELB Stns., July, 1970: P703 (4); P708 (22); P711 (17); P716 (5); P17 (1). ELB Stns., 1964: H41 (16); H42 (16); H43 (79); H45 (25). ELB Stns., 1975: P1c (15); P1b (46). ELB Stns., 1976: B12a (2); ELB Stns, 1977: B5a, Witty's lagoon - 1 female ov (7.0 mm), female ov (5.0 mm), male (5.0 mm) (slide mounts), + 14 additional females, CMN Cat. no. NMCC1991-2107; B5c (51).

Southern mainland, ELB Stns., 1955: M11, White Rock (10).

WASHINGTON

ELB stations, 1966: W34, Crescent Beach, LW sand (with *E. estuarius*) - 10 males, 19 females, 5 im.

Diagnosis. Female (5.0 mm): Head, rostrum short. Eyes small, lenticular, whitish, lacking pigment. Antenna 1, segment 2 with strong anterior marginal setae, lacking proximally. Antenna 2, segment 4 medium deep, hind margin with ~25 plumose setae, postero-distal lobe medium; segment 5 large, medium broad; flagellar segment 1 with single postero-distal plumose seta.

Mandible, palp segment 3 medium, with 11-12 posterior marginal comb spines. Maxilla 1, palp segment 1 short. Maxilla 2, inner plate with inner marginal setae only. Maxilliped, inner plate and outer plates broad; palp segment 2, medial lobe broad, not attaining tip of moderately broadened segment 3.

Coxa 1, and 2 small, squarish. Gnathopod 1, basis with few distal posterior marginal setae; segment 5 medium deep; segment 6 broadening distally. Gnathopod 2, basis with postero-distal marginal setae; carpus slender, elongate, postero-distal spines slender; segment 6 short, medially broadest.

Peraeopod 3, basis medium, hind margin with distal setae; segment 4 long, gently broadening distally; segment 5 medium deep, anterior margin with shallow proximal excavation, hind margin proximally with setae; segment 6 drop-shaped, margins slender-spinose. Peraeopod 4, segment 6, hind margin with 2-3 long plumose setae; segment 4 with strong anterior marginal oblique row of spines, hind lobe medium, with 2 postero-proximal, and 1 distal, spine cluster; segment 6 slender, with 2 anterior groups of spines and setae, and hind margin distally with single spines and setae.

Peraeopod 5, coxa, hind lobe deep, margin weakly setose; basis short broad, suborbicular, hind margin setose except distally; segment 4 short, broadest distally, with moderate anterior clusters and posterior rows of facial spines; segment 5 longer than wide, facial spines strong; segment 6 slender, with 2 anterior marginal and 3 posterior marginal clusters of slender spines and setae, apex slender-spinose. Peraeopod 6, coxa deep, hind lobe setose below; basis broad, with shallow distal lobe, hind margin setose proximally; segment 4 medium long, broadest distally, with 2 weak facial spine clusters; segment 5 broadest distally, with 2 medium posterior facial clusters of spines and distal marginal row of 8-10 spines, distal excavation medium; segment 6 medium, nearly straight, hind margin with 5-6 clusters of spines, a few distal spines long, split-tipped. Peraeopod 7, basis broad, suborbicular, hind margin nearly bare, with strong proximal cusp or tooth; segment 4 medium, widest distally, hind margin setose throughout; segment 5, anterior margin with 2 clusters of spines, tips clavate, distal free margin with small spine cluster; segment 6 medium broad, with 1 antero-marginal and 2 postero-marginal clusters of spines.

Pleon plate 3, hind corner weakly produced, acute, well exceeded by postero-dorsal pleosomal lobe. Uropod 1, peduncle with a few weak marginal spines, distally with 3-4 stout spines; rami subequal; inner ramus, posterior margin setose; outer ramus posteriorly with singly inserted and clusters of spines and setae. Uropod 3, outer ramus, terminal

segment medium; inner ramus with 4-5 inner marginal plumose setae. Telson lobes short, thick, with 5-6 dorso-distal and 4-5 inner marginal setae.

Distribution: From Prince William Sound, Alaska, southward along southeastern Alaska, British Columbia and Washington to southern Oregon, possibly to central California. It occurs bathymetrically from about mid-tide to shallow sub-tidal levels, in fine sand, mainly along open, surf-exposed beaches, but also on protected beaches; it co-occurs with *E. estuarius* in salinities as low as ~ 10‰.

Taxonomic commentary: *E. washingtonianus* is the type of a unique and moderately advanced N. American endemic group of species. It contains 3 other N. American endemic full species, as noted in the key, and a variety as noted below. The group is typical of high energy intertidal surf sands, but the subtidal members are less strongly armoured. This species complex is most closely related to *E. eous* group of western Pacific shores. As noted by Gurjanova (1962), it bears some resemblance to, and possible direct relationship with, *E. gurjanovae* (see histogram, p. 59).

Eohaustorius washingtonianus variant

Material examined.

BRITISH COLUMBIA.

North-central coast. ELB Stns., 1964: H48, Goose I., north beach, fine sand at LW level, 9.8 C., Aug. 5 - 17 males, 14 females, 1 immature. ELB Stns., 1959: N1, Open Bight, Rivers Inlet, coarse sand at LW level, Aug. 3 - 15 im., CMN Cat. no. NMCC1991-2095; N6, Bremner Beach, near Raynor Pt., fine sand at LW level, 10.0 C., Aug. 6 - 7 males, 9 females.

Taxonomic commentary. Bosworth (personal communication) briefly commented upon a somewhat anomalous feature of specimens of "*washingtonianus*" from the three stations listed above. This observation is here confirmed. In peraeopod 7, segment 2 (basis) bears a small but distinct postero-proximal cusp, typical of *E. washingtonianus*, *E. brevicuspis* and *E. barnardi* of N.orth American beaches, and *E. gurjanovae* of western Pacific shores (p. 47). However, the present variant resembles *E. barnardi* in having a single group of spines (excluding the antero-distal group) on the anterior margin of segment 5 of peraeopod 7. This northern variant differs from *E. barnardi* in its other specific characters (key, p. 37), but appears otherwise similar to material of *washingtonianus* from adjacent northern localities. We therefore conclude, tentatively, and on the basis of the limited material available, that specimens from the three stations above represent a local, mainly subtidal, variant of the typical form of *Eohaustorius washingtonianus* (Thorsteinson).

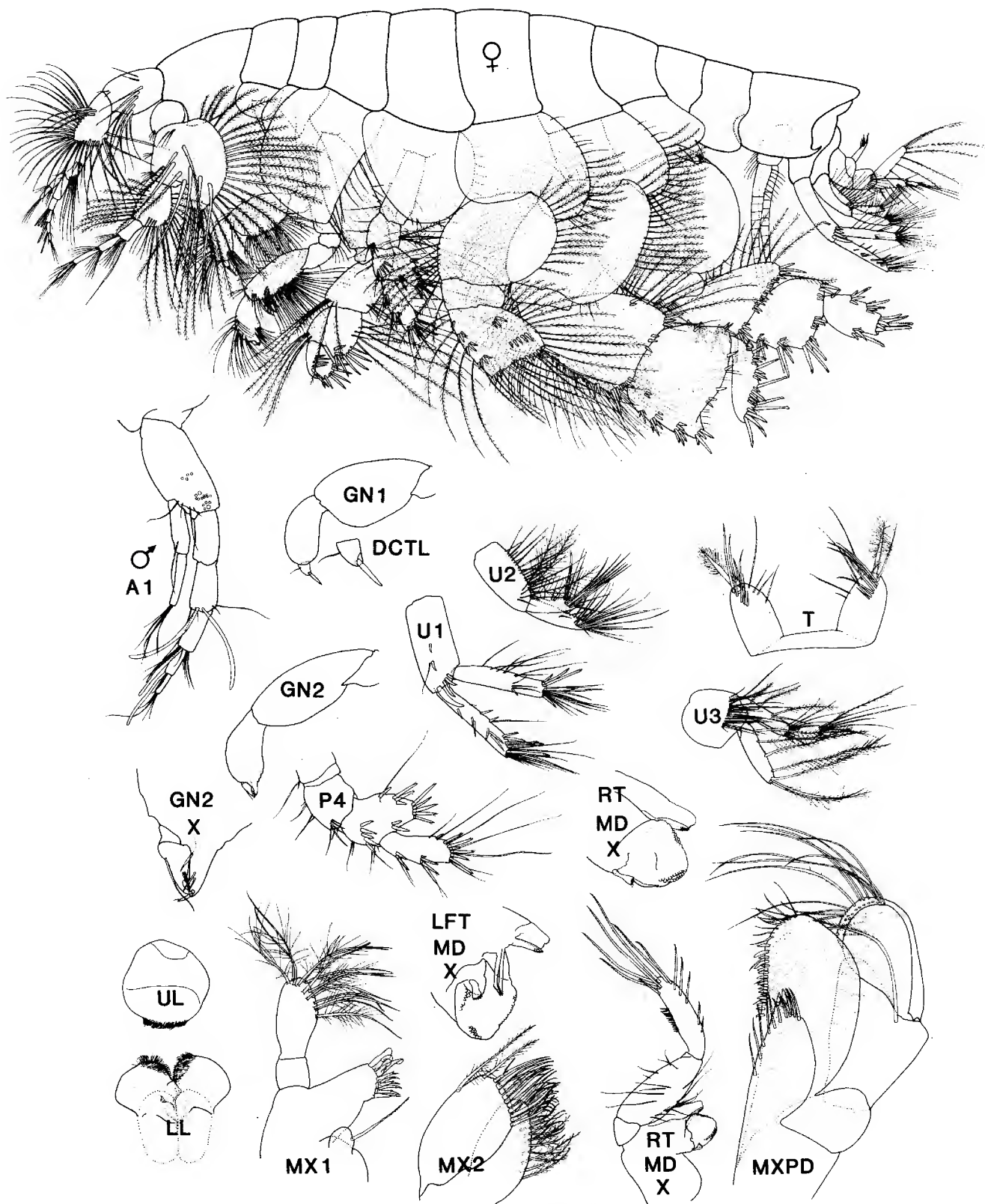


FIG. 11. *Eohaustorius washingtonianus* (Thorsteinson). Female (5.5 mm). Pt. Roberts, WA.

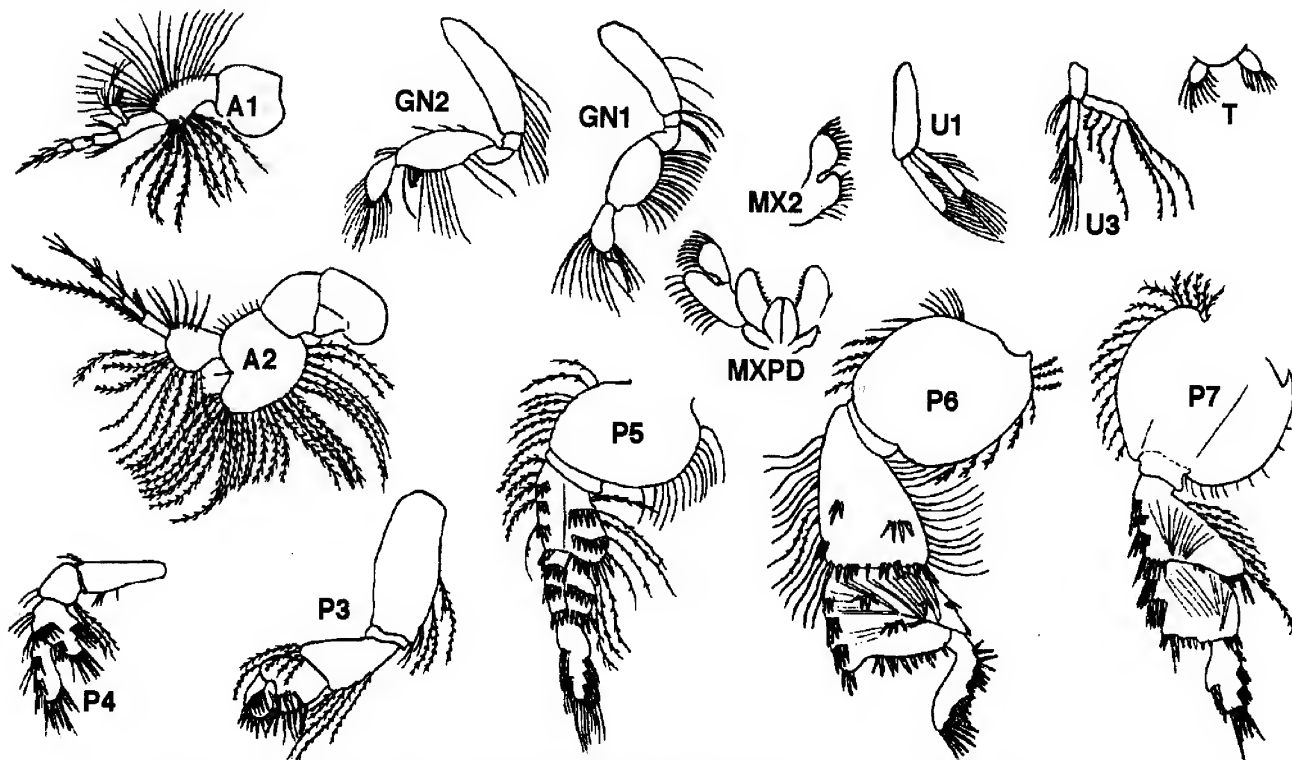


FIG. 12. *Eohaustorius washingtonianus* (Thorsteinson). Female (5.5 mm). Point Roberts, WA. (after Thorsteinson, 1941).

Eohaustorius barnardi, new species
(Fig. 13)

Eohaustorius washingtonianus J. L. Barnard, 1957: 82, plate 16.—Bosworth, 1974 (letter and manuscript to ELB).

Material. The species occurred in samples from the 1956 and 1959 "Velero" cruises near Pt. Conception, and further south, in depths of 5-20 meters (Barnard, loc. cit.).

The species was also collected by E. W. Fager from the end of the Scripps's pier in 1955-1956 (fide W. S. Bosworth).

Diagnosis. Female ov., **Holotype** (5.0 mm), 5 **Paratype** specimens, "Velero" Stn. 2312-53, collections of the Allan Hancock Foundation. Similar to *Eohaustorius washingtonianus*, with the following differences:

Mandible, palp segment 3, posterior margin with 9-10 (vs. 11) comb spines, and distal spines of outer margin more numerous (9-10 vs. 6-7). Maxilla 2, outer plate with 1 distal outer marginal plumose seta. Maxilliped, outer plate shorter, more slender; palp segment 3 less broadly expanded.

Gnathopod 1, segment 5 more deeply broadened distally. Gnathopod 2, basis, hind margin more heavily setose; segment 6 broadened distally.

Peraeopod 3, coxa, antero-distally angled, not rounded, lower margin nearly straight. Peraeopod 4, coxal plate subrectangular; segment 5, hind lobe short; segment 6 broadened medially.

Peraeopod 5, coxa shallower, hind lobe more richly setose behind; basis less broad; segment 6 relatively short broad, margins and apex with fewer spines. Peraeopod 6,

basis broadening distally; segment 4 slightly narrowing distally, facial spines few, weak; segment 5, facial spines few, distal excavation more pronounced. Peraeopod 7, basis with weaker proximal posterior cusp; segment 4 less broad distally; segment 5, anterior margin with 1 cluster of spines.

Pleon plate 3, hind corner more strongly produced, sharply acute, less exceeded by postero-dorsal process of pleon 3. Uropod 3, rami more slender, inner ramus with fewer inner marginal setae.

Taxonomic commentary. According to Bosworth (1973; personal communication), Barnard (1957, plate 1) incorrectly designated his subtidal material from southern California as *Eohaustorius washingtonianus*, mainly because of the pronounced cusp on the basis of peraeopod 7. However, Bosworth noted that the cusp is more strongly pronounced, and the ratio of segments 5 & 6 of peraeopod 5 is different in Thorsteinson's original northern species.

Other differences, noted in this study, include (in *E. barnardi*) the smaller size of maxilliped palp segment 3, the smaller size of the carpal lobe of peraeopod 4, the weaker facial armature of segments 4 & 5 of peraeopod 6, the less prominent hind lobe of segment 4 of peraeopod 7, and the more prominent and more strongly angled posterior process of pleon plate 3.

Etymology. We take pleasure in formally naming this species in honour of the late Dr J. L. (Jerry) Barnard who initially described and figured it, and who contributed inestimably to the advancement of knowledge of the systematics and biogeography of fossorial amphipod crustaceans.

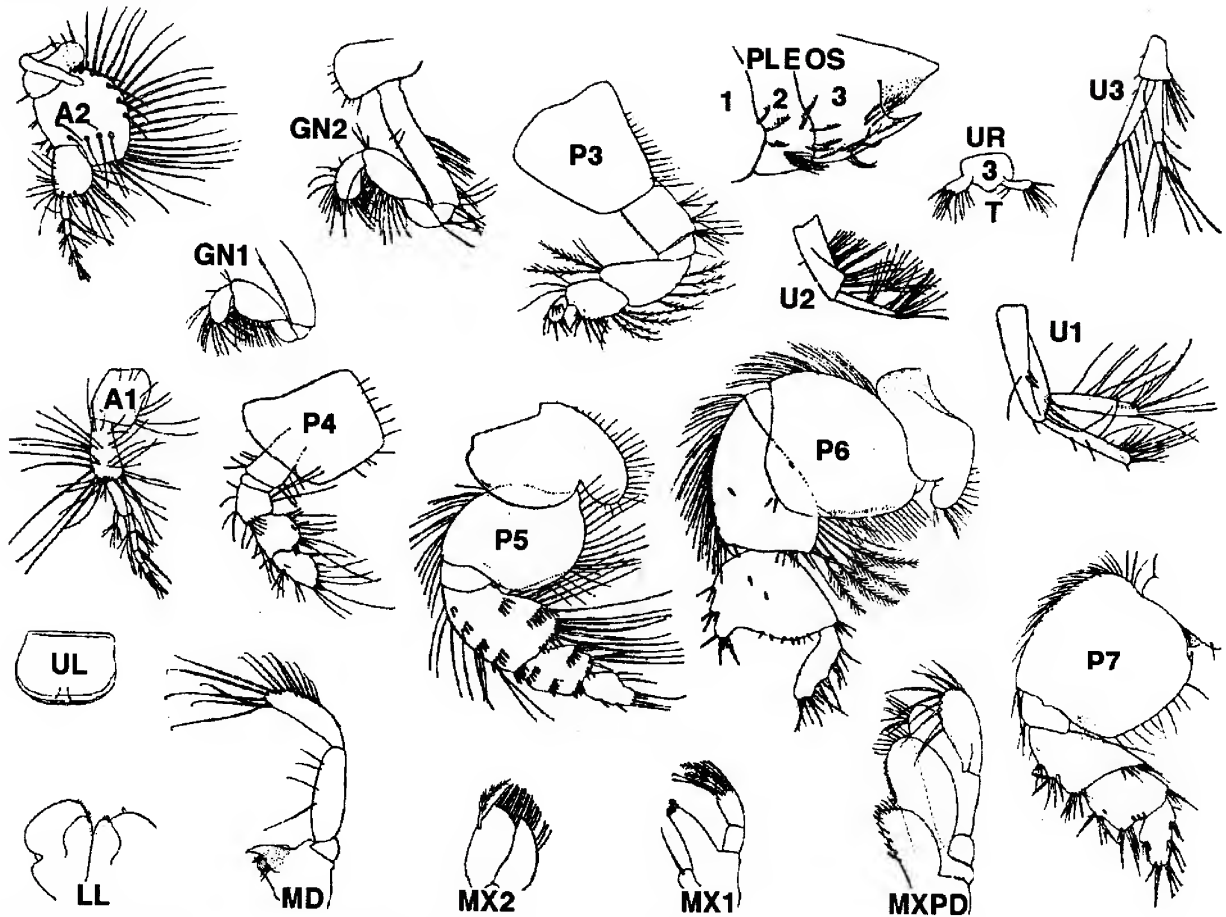


FIG. 13. *Eohaustorius barnardi*, new species. Female (5.0 mm). San Pedro shelf, ~15 m, California. (modified from Barnard, 1957).

Eohaustorius cheliferus (Bulycheva)
(Fig. 14)

Haustorius cheliferus Bulycheva, 1952: 198, fig. 3.

Eohaustorius heliferus Gurjanova 1962: 411, figs. 138A, B.

Eohaustorius cheliferus Barnard & Karaman, 1991: 363.—
Ishimarus, 1994: 64.

Diagnosis: Female ov (7.0 mm) Head broad, rostrum short, broadly acute. Eyes unpigmented. Antenna 2, peduncle 4, posterior lobe large, with 35+ marginal plumose setae, postero-distal lobe strongly produced, attaining end of segment 5; segment 5 broadest medio-distally; flagellar segment 1 with 3 postero-distal plumose setae.

Mouthparts undescribed.

Gnathopod 1, basis, hind margin weakly setose; segment 5 shallow, not elongate; segment 6 broadest medio-distally, dactyl stout, unguis linear, longer than body. Gnathopod 2, basis, posterior margin distally setose; segment 5 slender, postero-distal spines each with medial cross-piece, distally toothed; segment 6 slender, short.

Peraeopod 3, coxa lunate, hind corner acute; basis broad, margins distally setose; segment 4 medium, distally broad, hind margin richly setose; segment 5 deep, hind margin heavily setose; segment 6 drop-shaped, margins lightly spinose. Peraeopod 4, segment 4, anterior oblique

row with stout spines, posterior margin with 3 long setae; segment 5 with strong anterior oblique spine row, posterior lobe large, long, postero-proximal margin with 4 clusters of spines and long setae, distal free margin bare; segment 6 small, overhung by lobe of 5, with single anterior marginal spine cluster, posterior marginal spines continuous with apical spines.

Peraeopod 5, basis broadening distally, postero-distal lobe faint, hind margin fully setose; segment 4 long, little broadened, facial spine rows strong; segment 5 subquadrate, facial spines strong; segment 6 medium, with single anterior and posterior marginal spine groups. Peraeopod 6, basis broad, hind margin strongly convex, setose proximally; segment 4 medium, broadest subapically, with 4-5 clusters of facial spines; segment 5 slightly broader distally, with single facial spine cluster, distal free margin with 7-8 spines, distal excavation medium deep; segment 6 short, curved forwards, hind margin with longish simple-tipped spines. Peraeopod 7, basis broad, hind margin nearly straight, distally weakly setose, lacking proximal cusp; segment 6 triangular, broadest distally, hind margin setose; segment 5 longer than broad, anterior margin with 2-3 spine clusters, distal free margin short; segment 6 medium broad, anterior margin with 1, posterior margin with 2, spine clusters.

Pleon plate 3, hind corner acute, produced, apex acute slightly angled upwards; lower margin setose. Uropod 3,

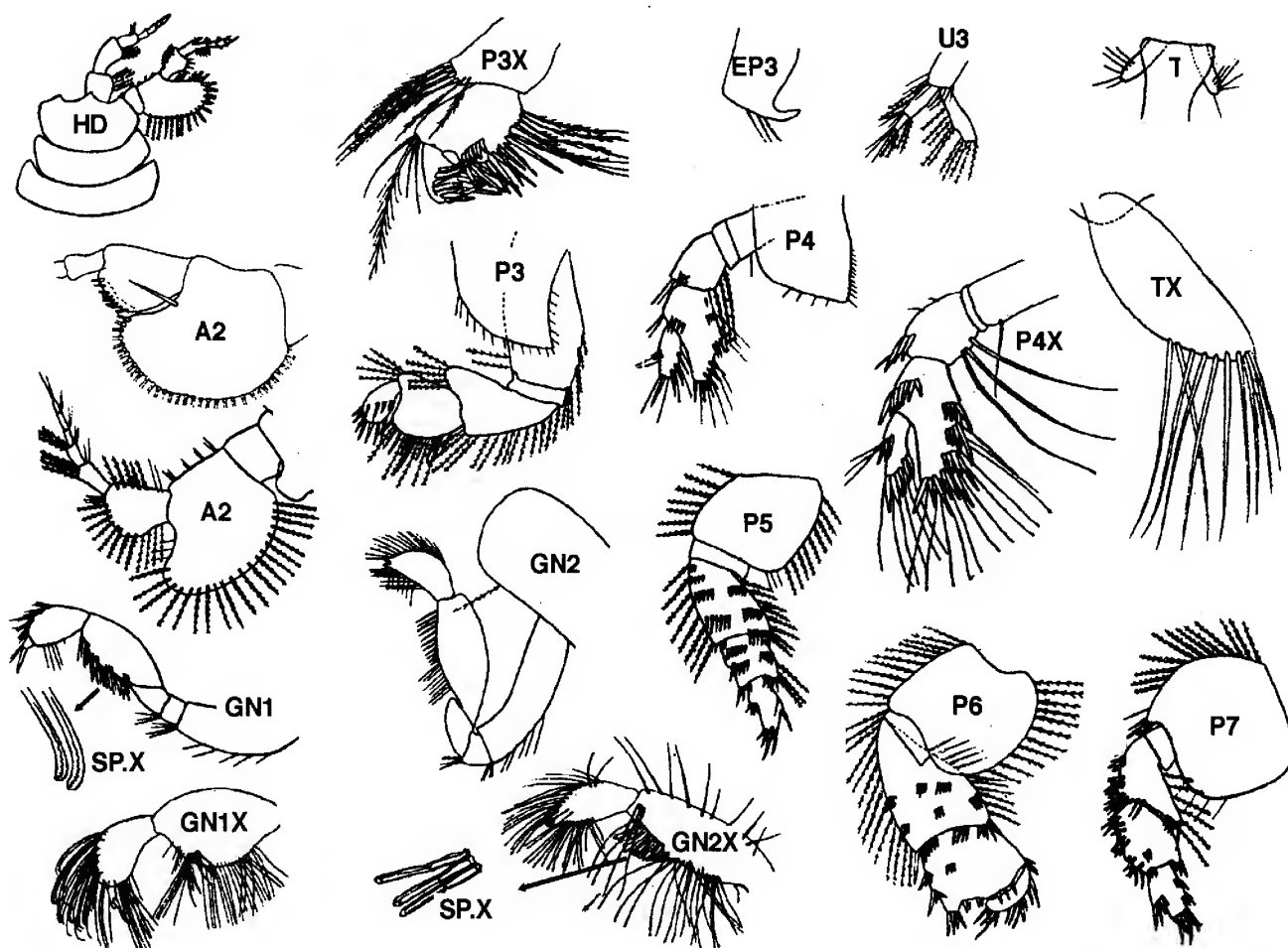


FIG. 14. *Eohaustorius cheliferus* (Bulycheva). Female ov (7.0 mm). Japan Sea to Sea of Okhotsk. (modified from Bulycheva, 1952)

rami medium; terminal segment of outer ramus medium; inner ramus, inner margin with 4-5 plumose setae. Telson lobes elongate, narrowly oval, with long dorso-distal setae.

Distributional commentary. Pacific coast of Iturup I, 30-40 m depth. Also recorded from the Sea of Japan (Peter the Great Bay) in depths of 0.75-13 m; also Sea of Okhotsk (Amur R. estuary and Aniv Bay) and Southern Kurile Strait, in depths of 6 - 40 m (Gurjanova, 1962).

Taxonomic commentary. The illustrations of Bulycheva (1952), repeated in Gurjanova (1962), are limited in detail but, in conjunction with her descriptive text, provide sufficient basis for reliable separation as a species distinct from all others of this study. As noted in the phenogram (p. 59) the species bears similarities to *E. longicarpus* of South Korean waters, and to *E. sencillus* of the North American Pacific coast, but is otherwise distinct from nearly everything else.

This species name may encompass a complex of closely related species. All materials listed by Gurjanova (1962) might therefore be re-examined for this possibility.

Eohaustorius longicarpus, new species
(Fig. 15)

Material examined.

Pusan, South Korea, protected and beach at LW, Jae-Sang Hong coll., June, 1983. - Female ov (4.0 mm) **Holotype** (slide mount); male (4.7 mm), **Allotype** (slide mount); female ov. (3.5 mm), **Paratype**. CMN Cat. no. pending.

Diagnosis. Female ov (4.0 mm): Head, rostrum. Eyes. Antenna 1, peduncle 1, anterior margin proximally bare. Antenna 2, peduncle 4, hind lobe deep, margin with 20-25 plumose setae, postero-distal lobe large; segment 5 medially deepest; flagellar segment 1 with 1-2 postero-distal setae.

Mandible, palp segment 3 slender, posterior margin with 10 comb spines. Maxilliped, inner plate broad medially; outer plate large, broad but short; palp segment 2, inner lobe broad, large, extending almost to tip of slender segment 3.

Coxae 1 & 2 small, medium deep. Gnathopods 1 & 2 generally similar to those of *E. cheliferus*.

Peraeopod 3 ordinary. Peraeopod 4, coxa relatively

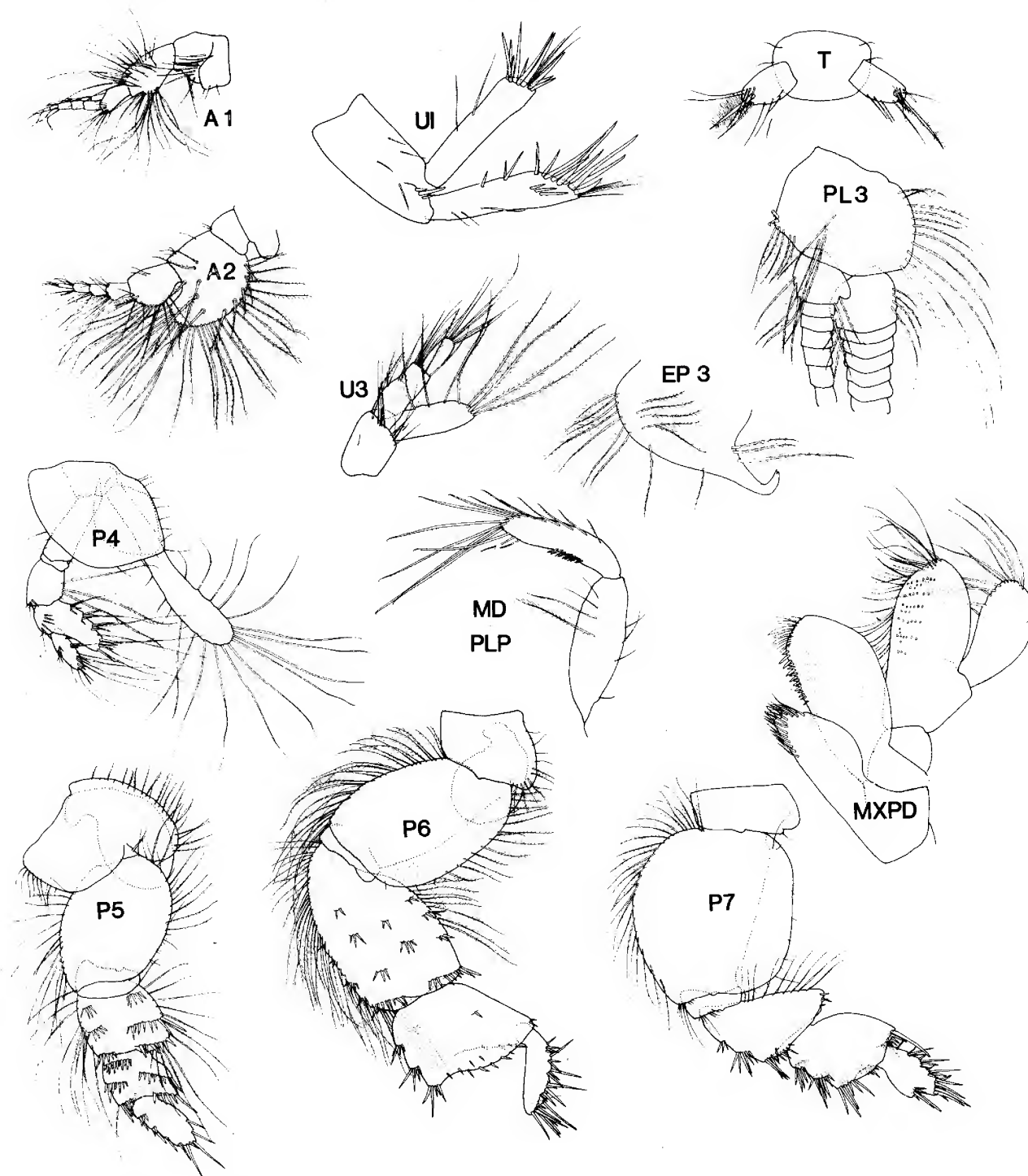


FIG. 15. *Eohaustorius longicarpus*, new species. South Korea. Male (4.5 mm); female (4.0 mm).

narrow, deep; basis slender, lacking distal setae; segment 4 with weak anterior oblique spine cluster, hind margin with 3 long plumose setae; segment 5 with anterior oblique row of slender spines, hind lobe elongate, proximal margin with 3 spine clusters, distal free margin bare; segment 6 slender, nearly exceeded by hind lobe of segment 5, anterior margin with 1, posterior margin with 2-3, groups of slender spines and setae.

Peraeopod 5, hind lobe of coxa narrow, deep, hind margin strongly setose; basis relatively slender, subovate,

lacking distinct postero-distal lobe; segment 4 short, uniformly broad, facial spine rows strong; segment 5 broader than long, facial spines strong; segment 6 broad, anterior margin with 3-4 singly inserted or groups of spines, hind margin distally with 2 slender spines. Peraeopod 6, basis little expanded distally broadest, with weak distal lobe, hind margin distally bare of setae; segment large, long, broad throughout, with 5-6 clusters of facial spines; segment 5 short, very broad distally, with 1 or 2 facial spines, and 5-7 distal margin spines, distal excavation very shallow; seg-

ment 6 straight, hind margin with 6-7 spines, long spines simple. Peraeopod 7, basis medium broad, hind margin nearly straight, nearly bare, lacking proximal cusp; segment 4 triangular, broadest distally, hind margin setose; segment 5 subquadrate, anterior margin with 2 spine groups, distal free margin with 1-2 small spine groups; segment 6 medium, broadest medially, anterior margin with 1, posterior margin with 3, clusters of slender spines.

Pleopods, peduncle large, broad; outer ramus with 15? segments, inner with 10 segments? Pleon plate 3, hind corner strongly produced, sharply upturned near apex, base of inner margin with 3 long setae. Uropod 1, rami subequal; peduncle, outer margin nearly bare, with 2-3 weak distal spines; inner ramus, posterior margin with 2 setae; outer ramus with a few posterior marginal spines. Uropod 3, rami relative short, thick, terminal segment long; inner ramus, inner margin with 4 long setae. Telson lobes short, thick, with 5-6 dorso-distal and a few inner marginal setae. Coxal gills short, saclike

Etymology. From *longi* - + *karpos* (wrist), alluding to the elongate posterior lobe of the carpus of peraeopod 4.

Distribution. Known only subtidally from sand beaches in South Korea.

Taxonomic and biogeographical commentary. The species exhibits mainly plesiomorphic character states, and clusters generally with the primitive *E. eous* complex (F.g. 16, p. 59). It is not closely related to any other species (well below 75% similarity levels) and the material is regrettably insufficient for biographic commentary.

Discussion and Conclusions

In this study, the genus *Eohaustorius* was found to encompass 13 described species that are endemic to intertidal and shallow subtidal waters of the North Pacific marine region. Their sediment-burrowing and filter-feeding life styles are accompanied by limb adaptations that are grossly similar to, but much more highly specialized than, those of members of the North-Pacific endemic talitroidean family Dogielinotidae from which they are now phylogenetically separated (Bousfield & Tzvetkova, 1982; Barnard & Karaman, 1991). However, members of the Dogielinotidae are more advanced phylogenetically in having strongly sexually dimorphic gnathopods, and utilizing pre-amplexing reproductive behaviour (Bousfield & Shih, 1994).

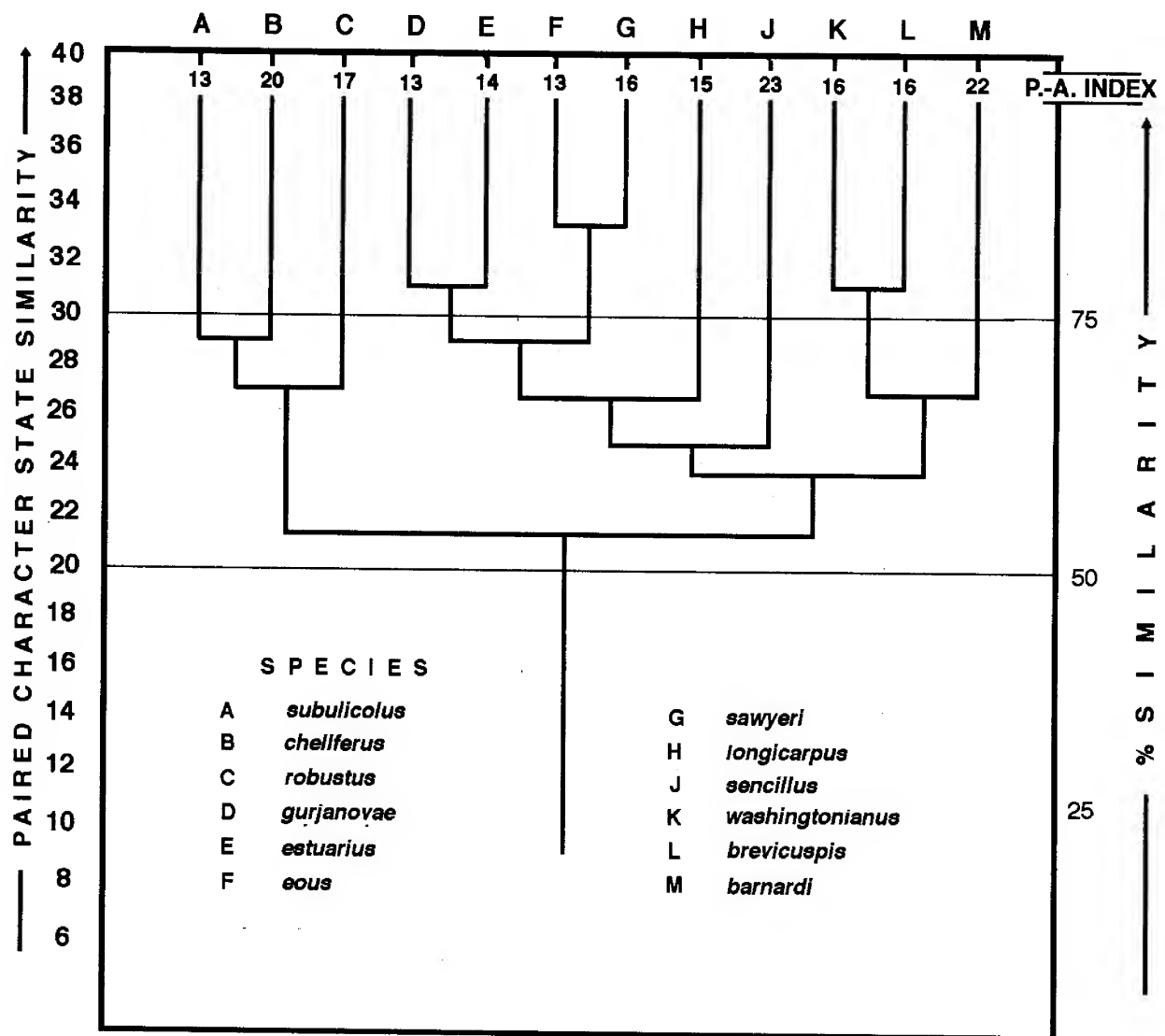
As noted previously (e.g. Barnard, 1957; Bousfield 1965), *Eohaustorius* is grossly similar in body form and limb structure to the 7 other genera of family Haustoriidae most of whose member species are endemic to the North American Atlantic region (Bousfield, 1970). However, the species of *Eohaustorius* are distinguished not only by their generally smaller size, but by their less highly specialized mouthparts, smaller coxae of gnathopods 1 & 2, unlike form of peraeopods 3 & 4, generally shorter, broader, and less spinose distal

segments of peraeopods 5-7, lack of a distal ventral lappet on urosome 1, more setose rami of uropod 3, and the widely separated (basally unfused) lobes of the telson, among other differences.

Concerning a common ancestry for these 8 genera, *Eohaustorius* appears least different from the genus *Pseudo-haustorius* Bousfield, 1965. Similar character states include those of: (1) antennae 1 & 2 (flagella short, few segmented); (2) maxilla 1 (weakly setose inner plate, lack of baler lobe); (3) maxilla 2 (plates relatively unmodified for filter feeding); (4) maxilliped palp (segment 3 claviform); (5) peraeopod 6 (segment 6 spatulate [vs. linear]); (6) pleon segment 3 (strongly produced dorso-distally, lateral plate acutely produced); (7) urosome 1 (peduncle and rami setose, weakly spinose); (8) urosome 2 (nearly occluded dorsally by urosome segments 1 & 3); (9) uropod 3 (terminal segment of outer ramus short) and (10) telson (lobes setose [vs. spinose]). Some of these character states (e.g., 6, 10), as well as the subrectangular form of segment 5 of peraeopod 6, are typical also of the genus *Acanthohaustorius*. Whether these similarities signify relatively close phyletic relationships or accrue mainly to similarities in lifestyle and habitat of component species is moot. If phyletic, morphological similarities would link two genera that appear to have little readily discernible biogeographical relationship (see p. 59). An alternative possibility, that the genus *Eohaustorius* evolved independently from a pontoporeiid ancestral group, and that the family Haustoriidae is therefore polyphyletic, receives little support from this analysis.

Within the genus *Eohaustorius*, numerical analysis of 20 selected morphological characters and pertinent character states of 12 of the 13 described species is summarized in a phenogram of species similarities (Table I; Fig. 12). The present modification of the UPGMA cluster analysis system of Sneath & Sokal (1973) has been used in similar studies of other North Pacific amphipod groups (e.g., Conlan, 1983; Jarrett & Bousfield, 1994). Here the analysis is slightly compromised by limited morphological information available concerning mouthparts of some western North Pacific species. Despite the unavoidable emphasis on character states that may reflect burrowing behaviour rather than phyletic relationships, the overall results are considered significant.

In the phenogram (Fig. 16) three main groups "cluster out" at better than 60% similarity levels. In the centre is a relatively primitive *eous* group of six species, from both Asiatic and North American coastal regions, having P.-A. indices mainly of 13-16, but 23 for the somewhat isolated *E. sen-cillus*. The core group is flanked on the left by the somewhat aberrant Asiatic *cheliferus* group, with P.-A. indices of 13-20, and on the right by the North American *washingtonianus* group, with P. A. Indices of 16-22. The *cheliferus* group is characterized by strongly produced and/or distally hooklike hind corner of pleon plate 3 relatively strongly spinose hind margin of segment 6 of peraeopod 5, slender telson lobes, low numbers of comb spines on mandibular palp segment 3, and well-developed hind lobe of segment 5, peraeopod 4. Members of the *washingtonianus* group have a proximal

FIG. 16. PHENOGRAM OF NORTH PACIFIC SPECIES OF *EOHAUSTORIUS**

* except. *E. tandeensis* Dang, 1968

cus on the posterior margin of the basis of pereopod 7, one spine cluster on the postero-distal margin of segment 5 of pereopod 4, and a relatively large maxilliped palp segment 3. The core *eous* group shows mainly plesiomorphic character states, including a relatively elongate, facially and marginally spinose, segment 4 of pereopod 6 that typifies most Atlantic genera of haustoriinids. *E. sencillus* is uniquely advanced in its very short antennal flagella, enlarged dactyl of gnathopod 1, and short maxilliped palp segment 3. All in all, few species pairings exhibit greater than 75% similarity and none is closely related, suggesting long periods of isolation and limited gene flow between populations. The relatively primitive nature of intertidal vs. subtidal species of *Eohaustorius* is consistent with similar trends in other regional fossorial amphipods (e.g. Jarrett & Bousfield, 1994a).

Biogeographical Considerations

The subregional occurrence of species of *Eohaustorius* is provided in Table II. Of the twelve species considered here, five are endemic to Asiatic North Pacific shores, and six to the North American coast. Only one species, *E. eous*, occurs in both continental waters, and only in the Bering Sea region.

In the Asiatic region, *E. robustus* and *E. cheliferus* are confined mainly to the Sea of Okhotsk and Kamchatka regions whereas *E. gurjanovae*, *E. longicarpus* and *E. subulicolus* have been recorded exclusively or mainly from southern Sakhalin Island and the Sea of Japan. In the more southerly region, these haustoriid species overlap distributionally, in similar sedimentary habitats, with members of the talitroidean fossorial family Dogielinotidae. The dogiel-

TABLE I. CHARACTERS AND CHARACTER STATES OF SPECIES OF *EOHAUSTORIUS*

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Antenna 2, peduncle 4, number of posterior marginal setae	<20	25	>30
2. Antenna 2, flagellar segment 1, number postero-distal long setae	1	2	3+
3. Mandibular palp segment 3, number of posterior marginal comb spines	10+	7	5
4. Maxilliped palp, segment 3, size	Large		Small
5. Peraeopod 3, coxal shape	Squarish		Semilunate
6. Peraeopod 4, hind lobe of segment 5	Short W>L		Long L>>W
7. Peraeopod 4, segment 5, hind lobe, distal marginal spines	Absent		Present
8. Peraeopod 5, length of segment 4	Long		Short
9. Peraeopod 5, shape of segment 5	Narrow		Wide
10. Peraeopod 5, segment 6, number of posterior marginal spines	2 - 3		1
11. Peraeopod 6, length of segment 4	Long L>>W		Short W=L
12. Peraeopod 6, segment 5, number of anterior marginal spine clusters	2		1
13. Peraeopod 6, segment 4, hind marginal spines	1+		0
14. Peraeopod 7, basis, proximal hind marginal cusp	lacking		present
15. Peraeopod 7, segment 5, number of anterior marginal spine clusters	2-3		1
16. Peraeopod 7 segment 6, number of posterior marginal spine clusters	3-4	2	1
17. Pleon plate 3, type of hind process	short	medium straight	long, hooked
18. Uropod 1, inner ramus, number of posterior marginal setae	5+	2	0
19. Uropod 3, size of terminal segment of outer ramus	Long		short
20. Telson lobes, form.	elongate		short

TABLE II. DISTRIBUTION OF NORTH PACIFIC SPECIES OF *EOHAUSTORIUS*

SPECIES	BIOGEOGRAPHICAL ZONES								
	1	2	3	4	5	6	7	8	9
<i>E. subulicolus</i> [^]	X								
<i>E. longicarpus</i> [^]	X								
<i>E. gurjanovae</i> [^]	X	x							
<i>E. cheliferus</i> [^]	x	X							
<i>E. robustus</i> [^]		X							
<i>E. eous</i> [^]		X	X						
<i>E. estuarius</i> *				?	X	X	X	?	
<i>E. washingtonianus</i> *				X	X	X	X	x	
<i>E. brevicuspis</i> *						x	X	X	
<i>E. sawyeri</i> *						x	X	X	x
<i>E. sencillus</i> [^]							X	X	x
<i>E. barnardi</i> [^]								x	X

ZONES: 1. Japan Sea and southward 2. Sea of Okhotsk region 3. Bering Sea -W.Alaska
 4. Southeastern Alaska 5. Northern British Columbia 6. Southern British Columbia
 7. Washington-Oregon 8. North & Central California 9. Southern & Baja California
 Ecology: * Intertidal; ^ Subtidal

inotid species, of similar or slightly larger size, tend to occur mainly intertidally, during summer months at least, along sandy beaches and in estuaries, often in very high densities (Kamihira, 1981; Bousfield & Tzvetkova, 1982). The northernmost beaches are subject to freezing and ice scour, especially during the winter and early spring, during which time the dogielinotids shift from the littoral to the infralittoral zone. The regional haustoriid species occur subtidally, at least during summer months, and probably year-round. Perhaps intense competition with the filter-feeding and "sand-licking" dogielinotids in summer, and rigorous physical conditions in winter, are factors that have apparently prevented evolution of Asiatic regional intertidal haustoriid species.

Along North American Pacific sandy shores however, the situation is strongly contrasting. Of the six species recorded from southeastern Alaska to southern California,

the four northernmost species, *E. estuarius*, *E. washingtonianus*, *E. brevicuspis* and *E. sawyeri* occur essentially intertidally and shallow sublittorally. As noted on page 59, and in figure 16, these northern species show mostly plesiomorphic character states and probably evolved early during the penetration of the genus into the North Pacific region. The two southernmost species, *E. sencillus* and *E. barnardi*, are strictly subtidal and their character states are significantly more advanced. However, the northern intertidal species and one southern subtidal species (*E. sencillus*) all co-occur in biogeographical zone 6 (Washington-Oregon), the very region in which the single North American dogielinotid species, *Probosciniotus loquax* (Barnard, 1967) occurs intertidally in great abundance (Hughes, 1982). This species, and *Eohaustorius brevicuspis*, co-occur intertidally on open surf sand beaches and are

presumed to be heavily preyed upon by shore birds, especially during late summer. However, despite these negative factors of competition and predation, intertidal haustoriids are able to occur commonly throughout zone 6, and indeed zones 4-9, almost certainly because of year-round near uniformity of coastal marine conditions; water temperature seldom fall below 5°C, and winter ice scour is non-existent (Thomson, 1981). These near-uniform physical conditions probably account for the relatively wide geographical range of the North American species, each of which occurs in 3-5 biogeographical zones vs. the 1-2 zones of the Asiatic species.

With respect to its overall biogeographical affinities, *Eohaustorius* is essentially a cold temperate genus and, in this respect, closer to the presumed para-ancestral pontoporeiid and perhaps distantly ancestral gammaroidean groups that are restricted to holarctic regions (Bousfield, 1970; Bousfield & Shih, 1994). In the North Pacific, members of the genus *Eohaustorius* occur well north of 60° north latitude, and into the Bering Sea region, but apparently not into arctic waters where the Pontoporeiidae dominate (Bousfield, 1987). In the western North Atlantic region, however, the 7 haustoriid genera are essentially temperate, and warm-temperate in thermal requirements. Species of the most eurytopic genus, *Haustorius*, range along North American shores north only to latitude 47° (southern Gulf of St. Lawrence) where they appear to be limited intertidally by the severity and duration of winter conditions (Bousfield, 1965). In western Europe, however, where winter conditions are relatively mild and reminiscent of those of the western north Pacific, the species *H. arenarius* attains 60° north latitude (southern Norway) (Lincoln, 1979).

In conclusion, we have noted on p. 59 that *Eohaustorius* is grossly similar morphologically to the North Atlantic complex of haustoriid genera, but is here found biogeographically unrelated to them. In absence of firm evidence to the contrary, the genus *Eohaustorius* is here surmised to have been isolated in the North Pacific for a considerable period of time. An hypothetical subtidal common ancestor may have connected it directly to the relatively primitive North Atlantic genus, *Pseudohaustorius*, possibly during the early Miocene epoch. At that time, the Panama isthmus had not yet formed and suitably cool marine connections existed between Atlantic and Pacific coastal marine regions (Adams, 1981). Although such an explanation is not entirely satisfactory, it does accord reasonably with rationale proposed for similar Pacific-Atlantic disjunct distributions in other amphipod groups. Thus, in some members of the fossorial phoxocephalid genus *Eobroglus* (Jarrett and Bousfield, 1994b) and in two species of the non-substrate modifying parapeleustid genus *Incisocalloipe* (Bousfield and Hendrycks, 1995), the distributional hiatus and its explanation may be similar, but the evidence for it appears to be more compelling.

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The Canadian Field-Naturalist

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The Canadian Field-Naturalist is the official publication of The Ottawa Field-Naturalists' Club and features both articles and notes on original research, and observations on the natural history of northern North America (including distribution, faunal analyses, taxonomy, ecology, and behaviour). Issues include news and comment (Club annual meetings and awards, tributes and review papers) and book review and new title sections. Since 1984, it has presented edited Status Reports for individual species designated by the Convention on Species of Endangered Wildlife in Canada (COSEWIC). It is entirely supported through club membership and subscriptions, page and reprint charges. The Ottawa Field-Naturalists' Club has 1041 members and The Canadian Field-Naturalist an additional 248 individual and 573 institutional subscribers, for a distribution of 1862 copies.

The Ottawa Field-Naturalists' Club was formed in 1879 by scientists from embryonic federal departments including the Geological Survey and the Dominion Experimental Farm, and leading amateurs; this type of mix remains its strength to this day. The Club quickly emphasized publication, and for seven years beginning in 1880, it annually issued the Transactions of the Ottawa Field Naturalists' Club. With volume 3 in 1887, the Transactions became a subtitle of Volume I of The Ottawa Naturalist, a monthly publication. With Volume 3 of The Ottawa Naturalist in 1889, the emphasis changed from local members' reports to national ones, and in 1919 the journal was renamed The Canadian Field-Naturalist (starting with Volume 33 which was Volume 35 of the Transactions but this subtitle was subsequently dropped). The issues per year were gradually reduced from 12 to 9 to 6 and eventually to 4, the latter beginning with Volume 67 in 1953. However, the annual number of pages increased, in 1988 (volume 102) reaching a record of 798 with a the largest single issue of 216 pages in 102(2). Since 1967, the Club has separately published a local (Ottawa area) natural history journal, Trail & Landscape, now also issued quarterly.

Submissions to The Canadian Field-Naturalist and predecessors have long been peer reviewed, first through a "Publishing Committee", later "Sub-editors", and then "Assistant Editors" until the designation "Associate Editors" was adopted in 1885 and maintained ever since. Currently, most submissions also go to at least one (and often more) additional reviewer(s). Associate Editors are listed in every issue and, since 1982, additional reviewers have been acknowledged annually in the Editor's Report. A formal publication policy was published in The Canadian Field-Naturalist 97(2): 231-234. "Advice to Contributors" is published in one or more issues annually. The current subscription rate is \$23 for individuals and \$38 for institutions. Postage outside Canada is \$5.00 additional. Subscriptions should be sent to The Canadian Field-Naturalist, Box 35069, Westgate P.O., Ottawa, Ontario, Canada K1Z 1A2. Manuscripts for consideration should be addressed to Dr. Francis R. Cook, Editor, Canadian Field-Naturalist, RR 3, North Augusta, Ontario, Canada K0G 1R0.

Francis R. Cook

THE AMPHIPOD FAMILY PLEUSTIDAE ON THE PACIFIC COAST OF NORTH AMERICA: PART III. SUBFAMILIES PARAPLEUSTINAE, DACTYLOPLEUSTINAE, AND PLEUSIRINAE. SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by E. L. Bousfield¹ & E. A. Hendrycks²

ABSTRACT

The gammaridean amphipod subfamily Parapleustinae Bousfield & Hendrycks, 1994, contains 28 described species of which 26 have been recorded from coastal marine regions of the North Pacific Ocean. From shallow coastal shelf waters of the both continental coasts are here described and figured the following taxa: *Parapleustes americanus*, new species; *P. ishmarui*, new species; *Chromopleustes lineatus*, new genus, new species; *Gnathopleustes serratus*, new genus, new species; *G. simplex*, new species; *G. trichodus*, new species; *G. pachychaetus*, new species; *Trachypleustes vancouverensis*, new genus, new species; *T. trevori*, new species; *Micropleustes nautiloides*, new genus, new species and *M. behningiodes*, new species. Also proposed for inclusion within the subfamily are *Commensipleustes*, new genus (type species: *C. commensalis* (Shoemaker, 1952); *Incisocalliope* J. L. Barnard, 1959 (revived status) (type species: *I. newportensis* Barnard, 1959). This genus contains eight species of which *Incisocalliope nipponensis* is newly described from the Sea of Japan. Also variously redescribed, or treated, are: *Gnathopleustes den* (J. L. Barnard, 1969b); *G. pugettensis* (Dana, 1853); *Incisocalliope newportensis* J. L. Barnard, 1959; *I. bairdi* (Boeck, 1871); *Chromopleustes oculatus* (Holmes, 1908); *C. johanseni* (Gurjanova, 1951); *Micropleustes nautilus* (J. L. Barnard, 1969b) and *M. behningi* (Gurjanova, 1938). *Dactylopleustes echinoides*, new species (subfamily Dactylopleustinae Bousfield & Hendrycks, 1994) is newly described and figured, and *Pleusirus secorrus* J. L. Barnard, 1969b (subfamily Pleusirinae Bousfield & Hendrycks, 1994) is redescribed and figured.

Taxonomically, the seven parapleustin genera were found to be morphologically distinctive, and not very closely similar. A modified phenetic cluster analysis indicated that the most southerly, temperate and subtropical genus *Incisocalliope* is phyletically most advanced, and that the mainly N. American cold temperate genus *Chromopleustes* is the most primitive, despite the relatively advanced nature of its mouthparts, and weakly sexually dimorphic gnathopods.

Biogeographically, of the 26 species of Parapleustinae recorded from the North Pacific region, 16 species (in seven genera) occur along the North American coast, nine species (in four genera) along Asiatic shores, and one species in the Hawaiian Islands, south central North Pacific. The genera *Parapleustes*, *Chromopleustes*, *Micropleustes*, *Dactylopleustes* and *Pleusirus* are Pan-Pacific, with approximately equal numbers of species on North American and Asiatic coasts. However, the genera *Trachypleustes*, *Gnathopleustes* and *Commensipleustes*, containing about a dozen species in total, are apparently endemic to the North American Pacific region. The isolated occurrence of *Parapleustes gracilis* (Buchholz, 1874), and *Incisocalliope aestuarius* (Watling & Maurer, 1973) in different temperature regimes of the North Atlantic region, appear anomalous. Although explanations proposed for such disjunct distributions are not entirely satisfactory, they underscore the high regional endemicity of subfamily Parpleustinae within the North Pacific Basin.

INTRODUCTION

Pleustid amphipods form an important assemblage of microcarnivorous amphipod crustaceans in the North Pacific marine region. Of the 12 recognized subfamilies (Bousfield & Hendrycks, 1994), the Parapleustinae, with nearly 30 described species, is one of the largest and numerically dominant groups in shallow-water habitats of both Asiatic and North America coasts. The monotypic subfamily Pleusirinae is common along the North American coast. Species of Dactylopleustinae are commensals on echinoid echinoderms, rarely encountered, and the subfamily probably more diverse than the three known species would indicate.

Prior to the present investigation, only eight species of subfamily Parapleustinae had been recorded from North American Pacific localities, all of which had been relegated to the genus *Parapleustes* by Barnard & Karman (1991).

Early 19th century records of Dana, Stimpson, Boeck and others had been capably summarized by Stebbing (1906). In the first half of this century, Holmes (1908) described *Pleustes oculatus* from off California. Few other records accrued until J. L. Barnard commenced his monumental series of studies (1952, 1954, 1956 *et sequ.*) on amphipod communities of the California coast. His paper with Given (1960) summarized information on five parapleustins known to that date, including *Parapleustes newportensis* Barnard, 1959, that had been described initially as the type species of a new genus, *Incisocalliope*. Shoemaker (1952) had earlier described *P. commensalis* from the pleopods of a spiny lobster off southern California, and later (1964, posthumously) added to records of Dana's "*Parapleustes pugettensis*" from Dillon Beach, California. Dana's species name was here found to embody several distinct taxa, mostly new to science. Barnard (1969b) described *Parapleustes den*, *P. nautilus* and *Pleusirus secorrus* from the Central California coast,

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and the following year (1970) added *P. derzhavini makiki* from the Hawaiian Islands. Very recently, Barnard & Karaman (1991) submerged *P. johanseni* Gurjanova, within *P. oculatus* Holmes, and synonymized *P. bairdi* (Boeck) and *P. newportensis* (Barnard) with *P. pugettensis* (Dana). The pragmatic illustrated keys of Barnard (1975), Staude (1987), and the regional annotated listing of Austin (1985), provide useful summaries of existing knowledge and bases on which to conduct further studies.

On the Asiatic Pacific coast, work on parapleustins commenced with Gurjanova's description of *Neopleustes derzhavini* and *Pleustes behningi* (1938) and *Parapleustes johanseni* (1951). Kudryaschov (1972) provided records of *P. nautilus* (later proven to be a new species). Tzvetkova (1975) described the echinoid commensal species *Parapleustes echinoicus*, later given separate generic status (as *Dactylopleustes*) by Karaman & Barnard (1979). Kudryaschov & Tzvetkova (1975) concluded the Russian contribution with a description of *Pleusirus secorrus asiaticus*.

Workers from Japan entered the western Pacific parapleustin scene with Irie & Nagata's preliminary regional listing (1962) of "*Parapleustes oculatus*" and "*P. pugettensis*". Ishimaru (1984) contributed most significantly with *Parapleustes dilatatus* n. sp., *P. longimanus*, n. sp., and records of *Parapleustes gracilis* Buchholz, *P. behningi* Gurjanova, and *P. derzhavini* Gurjanova. Soon after, Ishimaru (1985) added *Pleusirus secorrus* to the regional list. Hirayama (1988) described *Parapleustes filialis*, n. sp. and *Dactylopleustes obsolescens*, n. sp. Finally, Ishimaru (1994) treated the entire pleustid fauna of Japan in his useful regional catalogue of gammaridean and ingolfiellidean species.

The previous studies had revealed a significant new fauna of parapleustinids, pleusirins and dactylopleustins in the western Pacific and Californian regions. However, corresponding faunas of the enormous intervening coastal areas were virtually unknown. Based on extensive new material from the coasts of British Columbia, southeastern Alaska, and Washington and Oregon states, the present study attempts to fill this large hiatus in systematic knowledge. It also attempts to relate these faunas phyletically and biogeographically to faunas of adjacent regions and elsewhere.

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SYSTEMATICS

Family PLEUSTIDAE

PARAPLEUSTINAE, Bousfield & Hendrycks, emended

Parapleustinae Bousfield & Hendrycks, 1994: 41.

Type genus. *Parapleustes* Buchholz, 1874 (p. 67).

Genera. *Chromopleustes*, new genus (p. 73); *Comensipleustes*, new genus (p. 82); *Gnathopleustes*, new genus (p. 82); *Incisocalliope* J. L. Barnard (p. 95); *Trachypleustes*, new genus (p. 105); *Micropleustes*, new genus (p. 111); .

Removals. *Parapleustes assimilis* (Sars, 1883); *P. bicuspis* (Kroyer, 1838); *P. monocuspis* Sars, 1895; *P. gagarae* Gurjanova, 1972; *P. major* Bulychева, 1952, *P. bicuspoides* Nagata, 1965; *P. sinuipalma* Dunbar, 1947, *P. trianguloculatus* Bulychева, 1952; *P. tricuspis* Ishimaru, 1984, to genera within subfamily Neopleustinae (Bousfield & Hendrycks, 1994, and in prep.).

Diagnosis. Body generally small to medium, smooth above, not mucronate on pleon; external surface pattern often colourful or disruptive. Head, rostrum short, little or not exceeding rounded lateral head lobe. Eyes variable in size and form, usually medium large, subrotund. Antennae usually elongate; antenna 1 the longer, occasionally short, peduncular segments often shortened. Accessory flagellum minute.

Mouthparts generally strongly modified. Upper lip distinctly notched, lobes variously asymmetrical. Lower lip broad, squat, outer lobes oblique. Mandible, molar small, weak, thumblike, apex pilose, triturating surface lacking or

vestigial; blades generally numerous, often strongly modified: chisel-shaped, cusplike, or molarized in form; left lacinia wide, multidentate, cutting edge straight; right lacinia lacking; incisor multidentate, third (distal) tooth largest; palp segment 3 not shorter than 2, with basal "A" seta (of Cole, 1980). Maxilla 1, inner plate with single apical seta; outer plate with 9 (rarely 15-18) apical spine teeth; palp occasionally broadened, with distal facial setae, apices spinose; segment 1 often with lateral ("shoulder") seta(e). Maxilla 2 ordinary, inner palate with stout inner marginal plumose seta(e). Maxilliped: palp strong, segment 2 usually longest, 3 lacking distinct distal process; outer plate narrow (vertical margins subparallel), sparsely setose and/or spinose; inner plate short, apex with "button" spines, inner margin with few setae and/or spines.

Coxal plates large, deep, broad; coxa 1 generally broadening distally and rounded below; hind corners cusped. Gnathopods various: weak to medium strongly developed; gnathopod 2 slightly larger, differing slightly in form, and occasionally sexually dimorphic. Gnathopod 1, basis, margins variously setose; meral cusp weak; propod, palm usually oblique, convex, with median tooth.

Peraeopods 3 & 4 ordinary, normally spinose, dactyls short to medium. Peraeopods 5-7 homopodous; coxae medium deep, hind margins rounded, laterally smooth; segment 4 longer than 5 which it variously overhangs behind.

Pleon plates 2-3, hind corners acuminate, not produced. Pleopods medium strong, ordinary. Uropods 1 & 2 ordinary; peduncle of uropod 1 with prominent distolateral spine; rami elongate, outer shorter, margins and apex strongly spinose. Uropod 3, inner ramus markedly the longer, margins spinose.

Telson elongate, narrowing distally, keeled proximally; apex rounded; penicillate setae medio-distal.

Coxal gills variable, smaller and saclike anteriorly, larger, platelike posteriorly. Brood plates large, broad.

Distributional ecology. The subfamily is essentially endemic to eulittoral shelf habitats of the North Pacific region. However, three species occur in isolation elsewhere, viz., the northeastern North Atlantic, the western North Atlantic, and the Hawaiian Islands of the central North Pacific (see p. 131).

Taxonomic commentary. The Parapleustinae is closely allied to subfamily Neopleustinae (Bousfield & Hendrycks, 1994). The latter differs, however, in having a well-developed keeled rostrum, dorsal body processes, a short, nearly centrally keeled telson, large mandibular palp, and a distally oblique and processiferous maxillipedal palp segment 3. Also, component members of the Neopleustinae occur in deep cold waters of the Arctic, North Atlantic and North Pacific regions; none is intertidal.

Numerical taxonomic analysis of the Parapleustinae reveals a complex of 7 generic-level subgroups (Fig. 43, p. 127), the species of which are treated systematically below.

Parapleustes Buchholz

Parapleustes Buchholz, 1874: 337.—Stebbing 1906: 320.—Gurjanova, 1951: 648 (partim).—Barnard 1969a: 425 (partim).—Barnard & Karaman, 1991: 649 (part).

Type species. *Parapleustes gracilis* Buchholz, 1874.

Species composition (North Pacific). *Parapleustes ishmarui* (= *P. gracilis* Ishimaru, 1984) (p. 70); and *P. americanus*, new species (p. 71).

Diagnosis. Body small, smooth above. Head, rostrum very short; anterior head lobe subacute; inferior antennal sinus broadly incised. Eye medium, elliptical to roundish. Antennae slender, medium long, weakly setose. Antenna 1 typically the longer; peduncle 3 short; peduncle 1, distal process weak; accessory flagellum minute.

Mouthparts modified. Upper lip shallowly notched, lobes asymmetrical. Lower lip medium wide, squat; outer lobes thick, rounded, oblique. Mandible: molar reduced to a blunt setulose knob; incisor irregularly toothed, distal teeth smaller; left lacinia 8-10 dentate; blades 5-12 in row, stout, weakly molarized; palp slender, segment 3 with few (3-5), posterior marginal "D" spines; maxilla 1, outer plate with 9 mainly tall apical spines; palp not broadened, with ~4 apical spines and several oblique subapical (facial) setae. Maxilla 2, inner plate little broadened, with marginal plumose seta. Maxilliped, palp strong, dactyl strong, segment 3 lacking distal process; segment 2 largest; outer plate short, little or not longer than inner, 1(2) apical spines; inner plate with few apical button spines and few marginal setae.

Coxal plates wide, deeper than respective body plates; lower margins straight, hind notch(es) distinct; coxa 1 little smaller than 2, slightly expanded distally.

Gnathopods medium large, closely subequal, little or not sexually dimorphic; propods broadening distally, palms smoothly convex, usually with central median tooth, postero-distal angle with 1-2 clusters of spines not extending onto palm; hind margin smooth, about equal in length to palm; carpus usually short, hind lobe deep; postero-distal process of merus acutely produced; bases slender, antero-marginal setae distally restricted.

Peraeopods 3-7 slender, weakly spinose; segment 5 and dactyls slender, relatively long. Peraeopods 3-4, margins of segments 4-6 weakly spinose, lacking special setae. Peraeopods 5-7 regularly homopodous, bases broad, convex behind.

Pleon plates broad, deep, smooth behind, hind corners weakly acuminate. Pleopods strong, not sexually dimorphic. Urosome short; urosome 2 not occluded dorsally. Uropods 1 & 2 rami slender, tips spinose, usually extending beyond uropod 3. Uropod 1, peduncle with distinct latero-distal spine; rami subequal in length. Uropod 2, inner ramus the longer. Uropod 3, inner ramus markedly the longer.

KEY TO KNOWN GENERA OF SUBFAMILY PARAPLEUSTINAE

1. Gnathopods 1 & 2, palm of propod with median tooth present, variously developed; gnathopod propod, length of palm about equal to (or longer than) posterior margin; gnathopod propods, hind margin lacking setae (except some *Incisocalliope*); gnathopod 2, carpus always relatively short, anterior margin $< 1/2$ length of propod 3.
 —Gnathopods 1 & 2, propodal palm, median tooth lacking or very reduced; gnathopod propod, length of palm short, usually much less than posterior margin (except in some *Micropleustes*); propod, hind margin with 1 - 4 setae or setal groups; gnathopod 2, carpus usually elongate, anterior margin about equal in length to propod (except some *Micropleustes*) 2.
2. Antennae slender, flagella elongate, antenna 1 usually markedly the longer; peraeopods 5-7, segment 4 postero-distally overhanging segment 5 by less than $1/4$ length of segment 5; coxal plates 2 - 4 not exceptionally large and/or deep, distal portions of respective bases exposed below, hind cusps of coxae 2 & 3 single *Chromopleustes* (p. 73)
 —Antennae short, stout, subequal, flagella little (or not) longer than respective peduncles; peraeopods 5 - 7, segment 4 overhanging segment 5 postero-distally by nearly half length of segment 5; coxae 2 - 4 large and deep, totally masking respective bases, hind corners with 2-5 small cusps (rarely single) *Micropleustes* (p. 111)
3. Antennae short, flagellum: of A1 little longer than peduncle, of A2 shorter than peduncle; gnathopods 1 & 2, carpus very short, length less than $1/4$ that of propod, hind lobe small, narrow; pleon plate 3, hind corner with small hook *Parapleustes* (p. 67)
 —Antennae normally elongate, flagellum distinctly longer than respective peduncle; gnathopods, dorsal margin of carpus more than one-fourth length of propod, hind lobe about half as wide as its dorsal margin; pleon plate 3, hind corner acuminate, not mucronate 4.
4. Peraeopods 5-7, segment 6 broadened distally, anterior margin with stout spines, forming (with dactyl) a grasping organ; maxilliped, outer plate shorter than inner plate; coxa 1 not noticeably broadening distally, hind margin lacking proximal short spine(s) *Commensipleustes* (p. 82)
 —Peraeopods 5-7, segment 6 normally slender and spinose; maxilliped, outer plate slightly longer than inner plate; coxa 1 broadening distally, hind margin with proximal spine(s) 5.
5. Gnathopods large, strongly subchelate, variously sexually dimorphic; basis, anterior marginal setae confined to distal angle; antenna 2, peduncular segments not shortened, surfaces armed variously with clusters of short setae *Gnathopleustes* (p. 82)
 —Gnathopods medium subchelate, propod and carpus combined shorter than depth of coxa, not sexually dimorphic; basis, anterior margin often setose throughout; antenna 2, peduncular segments 4 & 5 shortened and/or bare of surface setal groups 6.
6. Antenna 1, peduncular segment 2 short, less than half length of segment 1; mandible, palp segment 2 weakly setose (6-7 setae); left lacinia 10-12 dentate; maxilliped, palp segment 3 lined medio-distally with short spines *Incisocalliope* (p. 95)
 —Antenna 1, peduncular segment 2 not shortened, length greater than half that of segment 1; mandible, palp segment 2 with numerous (10-15) medial setae; left lacinia 7-9 dentate; maxilliped, palp segment 3 lacking distal short spines *Trachypleustes* (p. 105)

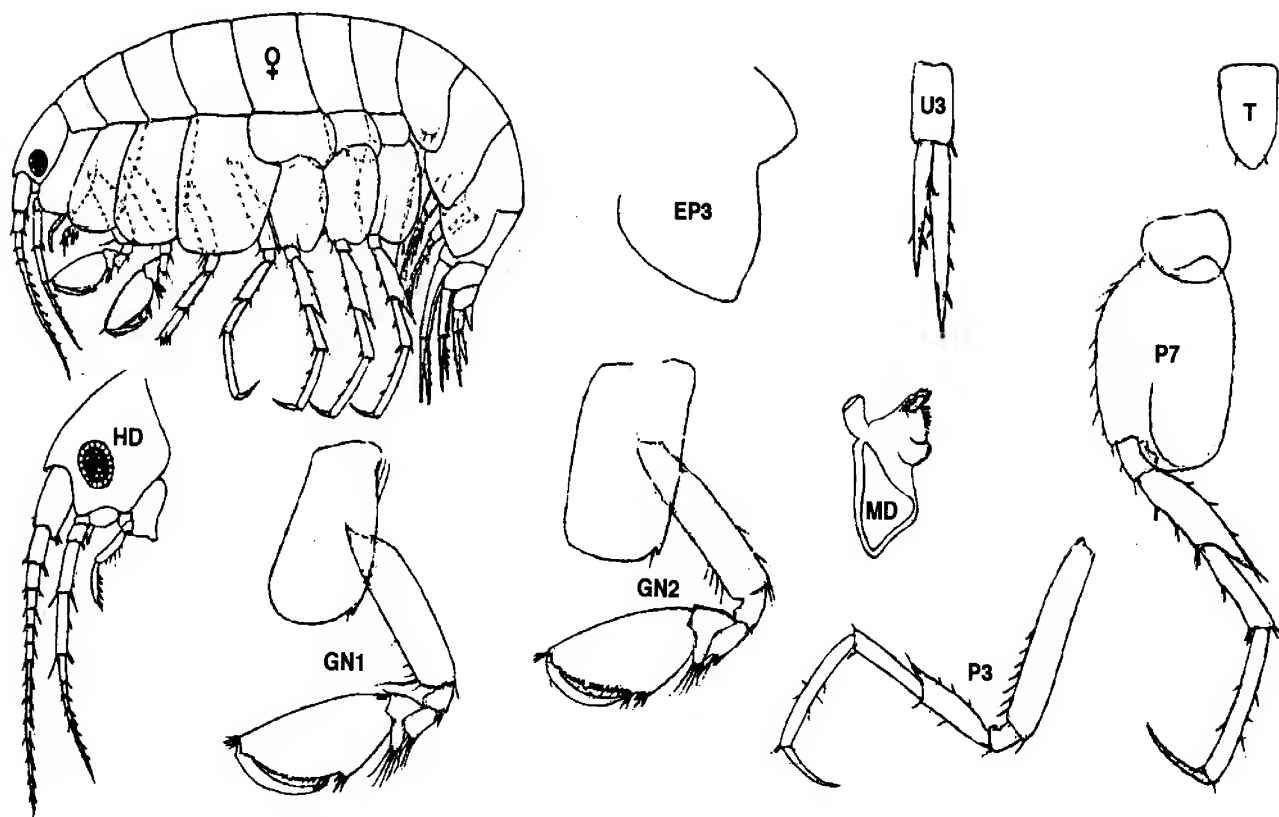


FIG. 1. *Parapleustes gracilis* Buchholz. Female (2.5 mm). Norwegian Sea. (after Sars, 1895).

Telson medium long, narrowing, subacute; dorsal penicillate setae slightly distad (of middle). Coxal gills sac-like, medium, unequal, smallest anteriorly.

Taxonomic commentary. The following species are removed from *Parapleustes*, sens. str.: *P. assimilis* Sars and *P. tricarinatus* Ishimaru (to *Neopleustes*); and *P. commensalis* Shoemaker (to *Commensipleustes*), for the following combination of reasons: lack of a disto-lateral spine on the peduncle of uropod 1; the pereopods are too long, or stout, dactyls too short; gnathopod propods are too slender, and/or the posterior margin is too strongly setose; the palmar tooth is lacking; the carpus is too long, shallow; the mouthparts are significantly different, especially in the mandibular blades; and the pleon is dorsally carinate.

Within *Parapleustes* proper, the markedly smooth propods and narrow carpal lobes of the gnathopods might suggest a closer relationship with the genera *Pleustes* and *Pleusymtes*.

Distributional commentary. The genus *Parapleustes* (sens. str.) is essentially arctic-subarctic in present distribution, dipping southward variably, and mainly subtidally in the North Pacific and northern North Atlantic regions. *Parapleustes gracilis* is not typical of the subfamily but became the type species because it is the only member occurring in the North Atlantic region where amphipod taxonomy began.

Parapleustes gracilis Buchholz

(Fig. 1)

Parapleustes gracilis Buchholz, 1874: 337, fig. 1.—Stebbing, 1906: 320.—Gurjanova, 1951: 648, fig. 444.—Barnard & Karaman, 1991: 650.

non Parapleustes gracilis Ishimaru, 1984.—Hirayama, 1988?

Paramphithoe brevicornis G. O. Sars, 1895: 353, pl 124. 2.

Diagnosis. Female (2.5 mm): Head, eye medium roundish, black. Antenna 1, peduncular segment 2 short, length ~1/2 segment 1; flagellum 13-segmented. Antenna 2, peduncular segments 4 & 5 slender, subequal; flagellum 8-segmented.

Mouthparts not described (not in Sars 1895, nor Stebbing, 1906) but probably similar to those of *P. americanus* (p.71).

Coxae 1-3 deep, medium broad, lower margins weakly convex, hind corners each with single cusp. Gnathopod 1, basis with weak antero-distal setal cluster; merus with acute postero-distal process; carpus short, hind lobe narrow, deep; propod distinctly expanding distally, inner face smooth; palmar margin oblique, convex, postero-distal angle with spine groups on either side of distinct dactyl-tip depression. Gnathopod 2 closely similar in size and form; basis, antero-distal margin with several setae.

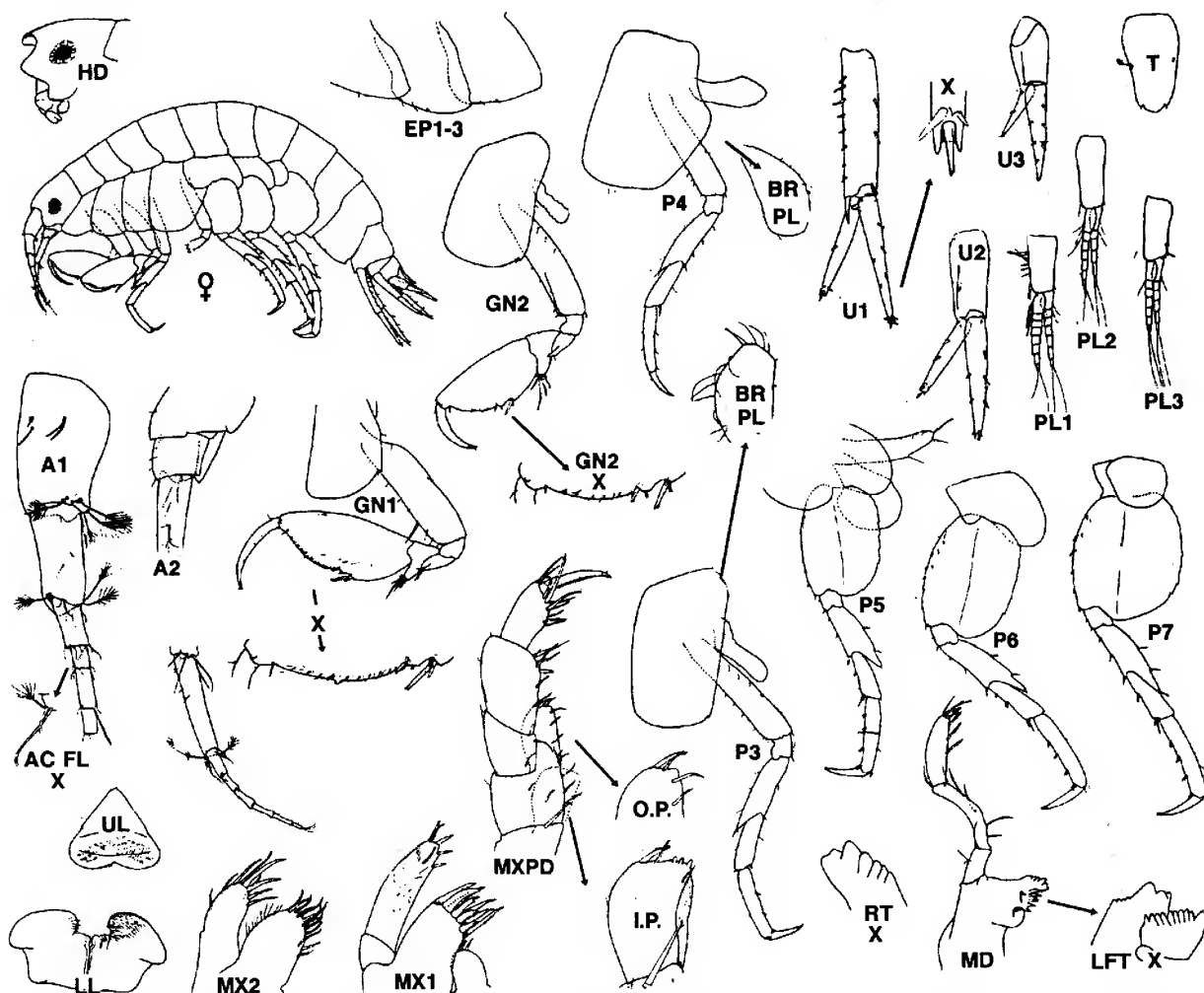


FIG. 2. *Parapleustes ishimarui*, new species. Female ov (2.4 mm) (= *P. gracilis* Ishimaru, 1984). Japan.

Peraeopods 3 & 4, bases with several antero-distal setae; segments 4-6 slender, elongate (especially segment 6); segments 4 & 5 subequal in length; marginal setae sparse; dactyl curved, elongate, length $> 1/2$ segment 6. Peraeopods 5-7 slender, bases medium broad, postero-distal lobes shallow; segments 4 & 5 subequal; segment 6 elongate; dactyl elongate, length $> 1/2$ segment 6.

Pleon plate 3, hind corner weakly acuminate, not hooked. Urosome 2 with free dorsal margin. Uropods 1-2 slender, peduncle and rami weakly spinose. Uropod 3, outer ramus $2/3$ length of slender inner ramus. Telson medium, length $\sim 1.5X$ basal width, apex subacute.

Distributional commentary. This species is endemic to arctic and arctic-boreal, North Atlantic waters. It has not been recorded authentically from the North Pacific region. As the type species of the genus, this North Atlantic form is included here for comparative purposes with North Pacific material previously ascribed to the name *Parapleustes gracilis* (above).

Taxonomic commentary. *Parapleustes gracilis* is the type of a small group of species here restricted to a few members of the North Atlantic and North Pacific pleustid

fauna. Of the 21 species of *Parapleustes* listed by Barnard & Karaman, most are members of subfamily Parapleustinae, but only *P. gracilis* (= *P. brevicornis* Buchholz?) is retained in the genus *Parapleustes*. All others are removed to other genera, and in some cases, other subfamilies. It has been found advisable to restore to the original position a number of transfers, and a number of synonymies, by others. Thus, *Micropleustes nautilus* is removed from the synonymy of *M. behningi*, and restored to full species recognition, and the genus *Incisocalliope* J. L. Barnard, 1959, is removed from the synonymy of *Parapleustes* Buchholz and restored to its original full generic position.

Parapleustes ishimarui, new species
(Fig. 2)

Parapleustes gracilis Ishimaru, 1984: 432, figs. 21-24.—
Ishimaru, 1994: 54.

Diagnosis. Female (2.4 mm): Head, eyes small, round, black. Antennae short. Antenna 1, peduncular segment 2 medium, length $> 2/3$ peduncular segment; accessory flagellum, apex rounded, with 1 plumose and 2 simple setae; flagellum 9-10 segmented. Antenna 2, peduncular segment

KEY TO KNOWN SPECIES OF *PARAPLEUSTES* (SENS. STR.)

1. A1, peduncle 2 short; pereopod 7, basis, posterior margin nearly straight; uropods 1 & 2, rami shorter than peduncle; pereopods 3 & 4, dactyls long ($>1/2$ propod) *P. gracilis* (Buchholz)(p. 69)
—Antenna 1, peduncle 2 normal; pereopod 7, basis, posterior margin strongly convex; uropods 1 & 2, inner ramus about equal in length to peduncle; pereopods 1 & 2, dactyls shorter ($<1/2$ propod) 2.
2. Pereopod 7, basis finely crenulate; pleon plate 3, hind corner forming small hook or mucrona; eye large, ovate; maxilliped, outer plate short *P. americanus*, n. sp. (p. 73)
—Pereopod 7, basis with few (8) large posterior notches along posterior margin; pleon plate 3, hind corner blunt-acuminate; eye small, round; maxilliped, outer plate normal, equal in length to inner plate *P. ishmarui*, n. sp (p. 71)

5 slender, slightly shorter than segment 4; flagellum short, 6-segmented.

Upper lip conical, apex shallowly incised, lobes slightly asymmetrical. Lower lip, inner lobes deep, not broad; outer lobes shallowly oblique. Mandible, molar prominent, slightly upturned apically; spine row with 6-7 short blades; cutting edge (left) with 3-4 large teeth proximally and 4 small denticles distally; palp segment 3, basal "A" setae short; postero-distal margin with 4 pectinate "D" spines; left lacinia 10-dentate. Maxilla 1, inner plate with single short seta; palp, apex sharply rounded, with 4 slender spines. Maxilla 2, inner plate broad, length nearly equal to outer plate, inner margin with short proximal seta. Maxilliped, inner plate broad, with 3 apical marginal "button" spines; outer plate medium, taller than inner plate, apex blunt, with 2 unequal slender spines; palp segment 3 slender, dactyl slender almost straight.

Coxae 1-3 lower margins gently convex, hind corners with single cusp. Coxa 4 hind marginal process rounded. Gnathopod 1, basis with weak antero-distal setae; merus with cusp; carpus short, hind lobe narrow, deep; propod expanding distally with weak inferior facial setae, palmar margin longer than convex posterior margin, postero-distal angle with weak distal and strong proximal spine groups adjacent to dactyl-tip depression. Gnathopod 2 closely similar in form but propod slightly smaller, and basis lacking antero-distal setal group.

Pereopods 3 & 4 regular, slender, segment 5 relatively short ($<$ segment 4), margins weakly spinose; dactyl short ($\sim 1/3$ segment 6). Pereopods 5-7 subsimilar, increasing slightly in size posteriorly; segment 4 and dactyl relatively short. Pereopod 7, basis more broadly expanded, hind margin weakly crenulate.

Pleon plate 3, hind corner subquadrate. Uropods 1 & 2 relatively short, margins weakly spinose, outer ramus distinctly the shorter. Uropod 3, outer ramus short, length $\sim 60\%$ stout inner ramus. Telson subrectangular, narrowing slightly distally, apex broadly rounded.

Type material. Ishimaru (1984): Female "a" (3.4 mm) **Holotype**; intertidal, Ohzuchi, Japan. Zoological Museum collections, Faculty of Science, Hokkaido University.

Distribution. Known from a single intertidal station, at Ohzuchi, Iwata Prefecture, northeastern Japan.

Etymology. The species is named in named in honour of Dr Shin-ishi Ishimaru who has contributed very significantly to knowledge of the marine amphipod fauna of Japan and adjacent regions.

Taxonomic commentary. *Parapleustes ishmarui* appears most closely related to *P. americanus* but differs in characters provided in the key (above).

Parapleustes americanus, new species
(Fig. 3)

Parapleustes pacifica (?) Austin, 1985: 592.—Barnard & Karaman, 1991: 650 (part).

Material examined:

ALASKA.

Bering Sea: N. E. of St. Lawrence I., P. Slattery, Dive 2, July 9, 1980 - 2 females. Punuk I., 5 m dive, gravel, P. Slattery coll., July 6, 1983 - 11 specimens, including females, males and im.

SE Alaska, ELB Stn. A48, Icy Strait, sand and gravel at LW level, June 17, 1948 - 5 females.

BRITISH COLUMBIA.

North-central coast: ELB Stn. H25 (Cox Pt. Inlet), 6 m dredge, muddy sand, July 18, 1964 - 7 im; H48 (Goose I.), 8 m dredge, sand, kelp, Aug. 5, 1964 - 2 females. **Paratypes** (slide mounts), CMN Cat. no. NMCC1955-0082. Swanson Bay, C. Levings Stn. 51B-031, Apr. 4, 1973 - 1 im.

Vancouver I., north end: ELB Stn. V20 (Brown Bay), coarse sand at LW, June 22, 1959 - 1 female ov, **Holotype** (slide mount), CMN Cat. no. NMCC1995-0081.

Vancouver I., south end: ELB Stns., July 5, 1976: B16 (off Bordelais I.), 44-50 m dredge, sand and gravel - 4 females ov.; B20 (off Long Beach, Trevor Channel), 30 m dredge, gravel - 2 females ov.

Diagnosis. Female ov (3.0 mm): Head, eye medium large, nearly round, black. Antenna 1, peduncular segment 2 long, length nearly equal to segment 1; flagellum 15-segmented. Antenna 2, peduncular segments 3 & 4 slender, subequal; flagellum 10-segmented.

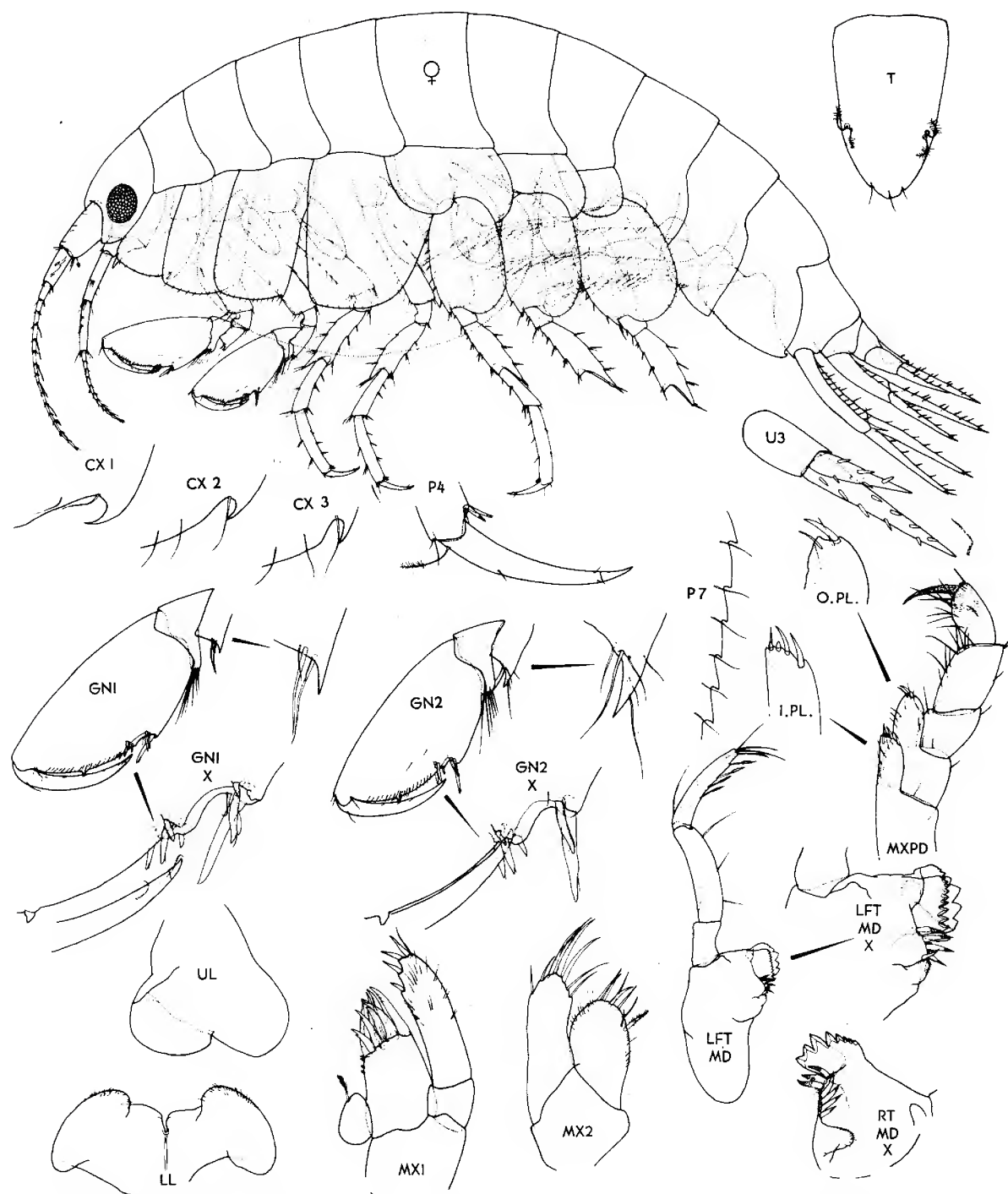


FIG. 3. *Parapleustes americanus*, new species. Female ov (3.0 mm). Brown Bay, B. C.

Upper lip, epistome tall, lobes asymmetrical. Lower lip, inner lobes medium broad, outer lobes normally oblique. Mandible, molar small, thumblike; spine row with 5-7 medium blades; incisor, cutting edge with 8 distally small teeth; palp segment 3 slender, basal "A" seta elongate; inner distal margin with 4 pectinate "D" spines; left lacinia 10-dentate, distal teeth small. Maxilla 1, inner plate with single apical seta; palp, apex obliquely truncate, with 4 slender spines. Maxilla 2, inner plate short, broad, inner margin with single plumose seta. Maxilliped, inner plate with single inner

marginal seta, and 1 apical marginal button spine; outer plate short, apex with single curved spine; palp segment 3 large; dactyl slender, nearly straight.

Coxae 1-3 medium broad, lower margins slightly convex, hind corners each with single prominent cusp. Gnathopod 1, basis with antero-distal setal cluster; merus, postero-distal process strong; carpus short, deep, hind lobe narrow; propod medium large, subovate, slightly expanding distally, length ~ 2X depth, inner face smooth; palmar margin oblique, convex, postero-distal angle with clusters of 4 spines on

either side of pronounced dactyl-tip depression; dactyl slender, with short terminal nail. Gnathopod 2 closely similar, propod slightly smaller.

Peraeopods 3 & 4 slender, segment 5 long (~ segment 4) marginal spines slender; dactyls medium long. Peraeopods 5-7 slightly increasing in size posteriorly; bases medium broad, postero-distal lobes medium deep, hind margins gently convex; distal segments slender, segment 5 long (~ segment 4); dactyls medium.

Pleon plate 3, hind corner with small hook. Uropods slender, spinose. Uropod 1, outer ramus slightly the shorter. Uropod 2, outer ramus distinctly the shorter. Uropod 3, outer ramus short, length ~60% slender inner ramus having 5=4-5 pairs of marginal spines. Telson narrowing gradually to subacute apex.

Distribution. From the Bering Sea, and southeastern Alaska to southern British Columbia, subtidally to depths of 50 m at southern locations, mainly on coarse sand and gravel bottoms.

Etymology. The species name alludes to its distribution along the American coast of the North Pacific Ocean.

Taxonomic commentary. In most character states, including the gnathopod propods and the unshortened segment 5 of peraeopods 3 & 4, *Parapleustes americanus* is similar to the type species, *P. gracilis*, from the North Atlantic region. These two species had been synonymized by Barnard & Karaman (loc. cit.). However, in *Parapleustes americanus*, the hind cusps of coxae 1-3 are more pronounced, urosome 2 is nearly occluded dorsally and, in uropod 3, the inner ramus is relatively short.

Some morphological differences have been noted between material from the Bering Sea and from southern parts of its range in British Columbia. These are here considered regional variations, not of species significance.

Chromopleustes, new genus

Parapleustes Stebbing 1906: 312 (part).—Gurjanova, 1951: 648(part).—Barnard 1969a: 425 (part).—Barnard & Karaman, 1991: 649 (part).

Parapleustinae: *oculatus* group, Bousfield & Hendrycks, 1994:42.

Type species. *Parapleustes oculatus* Holmes, 1908.

Species composition. *Chromopleustes johanseni*, Gurjanova, 1951; *C. lineatus*, new species (p. 78).

Etymology. a combining form of the Greek "*kromos*" referring to the remarkably disruptively banded and striped external body colouration, and the generic name "*Pleustes*".

Diagnosis. Body smooth above. Head, rostrum very short; inferior antennal sinus short, nearly right-angled.

Eyes large, nearly round. Antennae well-developed, slender, very weakly setose and/or spinose; flagella elongate. Antenna 2 distinctly the shorter; accessory flagellum extremely minute or lacking.

Mouthparts strongly modified. Upper lip deeply notched, lobes markedly asymmetrical. Lower lip very wide, deep, outer lobes slender, rounded very oblique. Mandible, left incisor with numerous (>15), right incisor with 9-12, dentations or serrations; left lacinia multicusate (>20); blades tall, slender, numerous (10-15), some with basal "satellite" setae; palp segments relatively short, segment 2 medially sparsely setose. Maxilla 1, apical spines of outer plates numerous (13-17), slender tall; inner plate with single minute apical seta; palp distally widened, with 6-8 apical spines and several closely subapical setae. Maxilla 2, inner plate not broadened, inner marginal plumose setae slender. Maxilliped, segment 3 (outer plate segment) strikingly enlarged, much longer and larger than palp segment 1; segments 2 & 3 short, dactyl strong; inner plate with 2-3 stout inner marginal setae.

Coxal plates medium, little (or not) deeper than corresponding body plates; coxa 1 not broadened or bent distally; postero-distal notch single, minute. Gnathopods small to medium strong, distinctly sexually dimorphic; propod and carpus elongate (especially in female), shorter, broader and stouter in male; palm of propod much shorter than posterior margin, straight, oblique, lined with short setae, lacking median tooth; carpal lobe shallow, medium to broad. Gnathopod 1, basis with proximo-posterior "hump".

Peraeopods 3-7 stout, medium long, weakly spinose, segment 5 strong; dactyls short, strong. Peraeopods 3 & 4, margins weakly spinose, lacking special setae. Peraeopods 5-7 regularly homopodous, bases somewhat narrowed behind.

Pleon side plates very broad, medium deep, hind corners acuminate but not produced. Pleopods normal, strong, not sexually dimorphic. Urosome short, segment 2 not occluded dorsally. Uropods regularly spinose; rami of uropods 1 & 2 distinctly longer than respective peduncles; outer ramus slightly the shorter. Uropod 3, rami much longer (3X) than peduncle, outer ramus distinctly the shorter. Telson medium-long, rounding apically. Coxal gills large, platelike.

Taxonomic commentary. Within the subfamily Parapleustinae, the genus *Chromopleustes* appears to be closest morphologically to the genus *Incisocalloipe*, on the apomorphic side, and to *Gnathopleustes* on the plesiomorphic side. It is distinguished from the latter, however, rather superficially by the more slender antennae; longer, less spinose legs with shorter dactyls; more elongate uropods, and more striking, disruptive body colouration. In detailed characterization, it is most distinct (unique) in the form of the mouthparts, with specialized proliferation of pectinate spines, blade spines, and multi-dentate incisors and lacinia mobilis.

To date, members of the genus have not been recorded outside the North Pacific coastal marine region, on both Asiatic and N. American coasts.

KEY TO KNOWN SPECIES OF *CHROMOPLEUSTES*

1. Eye small, remote from anterior head margin; antenna 2, flagellum <30-segmented; uropod 3, inner ramus with few (4-5) pairs of marginal spines; maxilliped, palp segment 1 longer than 2; Asiatic Pacific *C. johanseni* (p. 77)
- Eyes large, near anterior head margin; antenna 2, flagellum >30-segmented; uropod 3, inner ramus with 8-10 pairs of marginal spines; maxilliped, palp segment 1 shorter than 2; North American Pacific .. 2.
2. Gnathopod 2, propod slender (both sexes), length >2X depth; telson elongate, length >2X width; mandible, left lacinia with about ~40 marginal teeth; maxilliped, inner plate with 3 inner marginal setae; telson elongate, length >2X width *C. oculatus* (p. 74)
- Gnathopod 2, propod stout (both sexes), length <2X depth; telson short, length ~1.5 X width; mandible left lacinia with about 20 marginal teeth; maxilliped, inner margin with stout single blade adjacent to facial seta; telson short, length ~1.5 X width *C. lineatus* (p. 78)

***Chromopleustes oculatus* (Holmes)**
(Fig. 4, 5, 6, 7)

Neopleustes oculatus Holmes, 1908: 531, figs. 36, 37.

Parapleustes oculatus Barnard & Given, 1960:1.—Barnard, 1969b: 198 (key).—Bousfield, 1985: 31, fig. 1.—Stauder, 1987: 379.—Barnard & Karaman, 1991: 650.

Material examined: Nearly 60 specimens in 15 lots ALASKA. (numbers of specimens in parentheses): Bering Sea: Amchitka I., Aleutians Ids., C. E. O'Clair Sta. IA-2, Oct. 23, 1972 - 1 im.

Southeastern Alaska, ELB Stns, 1961: A3(70); A6(2); A18(2); A57(1); A168 (8); A174 (13); A175 (31); Stn. A8 (Tongass Narrows, opposite Ketchikan), rock and sand at LW, June 3, 1961 - 1 male (slide mount), (fig'd); female ov. (slide mount), (fig'd specimen), + 15 male, female specimens. ELB Stn. S19B1 (Kamen Pt., near Sitka), July, 1980 - 1 male, 2 im.

K. E. Conlan Stns., 1989: Torch Bay, 4.6-13.7 m, June 18 - male, female; Baranof I., Whale Bay, 4.5 - 6 m, June 21 - 1 male; Boca de Quadra, 30.5 m dredge, June 27 - 3 females; Frederick Sound, Brothers I., 5-6 m., P. Slattery coll., Mar. 24, 1988 - 8 males, females.

BRITISH COLUMBIA.

Queen Charlotte Island, ELB Stns, 1957: N2a (Parry Passage) 22 males, females; W8 (2); W15b(2). Naden Harbour, 9 m dredge, Sept 16, 1955 - 1 female.

North-central coast: ELB Stns, 1964: H3 (40); H5 (50); H7(6); H12(14); H29 (15); H33(30); H50 (60); H53 (16); H57 (2); H65 (7).

South-central coast: Sutton I., Sechart Narrows, 15 m dive, Neil McDaniel coll., July, 1978 - 1 male, 1 female, 7 im.

Vancouver I., north end: ELB Stns., 1959: O3 (15); O5 (9) O7b (15); V20 (Brown Bay) (9); V5 (Nigei I.) (2).

Vancouver I., south end: ELB Stns. 1955: F1 (1); F2 (1); F4 (3); P4 (9); P7 (2); ELB Stns., 1976: B4 (1); B5 (2); B8 (5); B21b (1).

CALIFORNIA:

Off Del Mar, 20 m, R. Rosenthal coll., June, 1969 - 6 im.

Diagnosis. Male (8.2 mm): Head, eye large, broadly ovate, black. Antenna 1, flagellum with ~60 small segments; accessory flagellum minute. Antenna 2, peduncle 5 distinctly longer than segment 4; flagellum with ~45 small segments.

Upper lip, median notch V-shaped, half depth of labrum. Lower lip, inner lobes very broad. Mandible, spine row with 14-15 slender blades; incisor cutting edge nearly straight, with 25+ teeth, strongest proximally; left lacinia, cutting edge slightly concave, with ~50 fine teeth; palp segment 3 with 12 pectinate inner marginal and 3 long terminal setae. Maxilla 1, inner plate with single short apical setae; outer plate with 12-13 slender apical spines; palp segment 2 slightly widening distally, with 8-9 apical short spines. Maxilla 2, outer plate not wider than inner. Maxilliped, inner plate medium, with 3 ordinary inner marginal setae and 5 small apical denticles; outer plate medium, apex obliquely truncated; palp segment 1 shorter than 2.

Coxae 1-3 relatively narrow, lower hind corner of each with minute cusp. Gnathopod 1, hind margin of basis with distinct proximal "hump"; carpus short, slightly longer than deep; propod slender, longer than deep; palm margin oblique, convex, merging imperceptibly with hind margin, postero-distal angle with 3+1 groups of short spines. Gnathopod 2, carpus short, little longer than deep; propod slender, length >2X depth; palmar margin very oblique, merging with hind margin, postero-distal angle with 4 groups of spines and 2 singly inserted spines.

Peraeopods 3 & 4 slender; segment 6 with 8-10 posterior margin spine groups; dactyls very short, little curved. Peraeopods 5-7 closely homopodous in form and size; bases not strongly broadened, lower hind lobes shallow; dactyls very short.

Pleon plate 3, hind corner weakly acuminate. Uropods 1-3 relatively long, inner ramus >peduncle, margins strongly spinose. Uropod 3, inner ramus >2.5 X peduncle, margins with 10-12 serial spines. Telson linguiform, length ~2X width, apex rounded.

Distribution. The species ranges from the Bering Sea and southeastern Alaska, south through British Columbia, to California, commonly from LW level to depths of 20 m, in a variety of habitats, associated with *Ulva* and bryozoans.

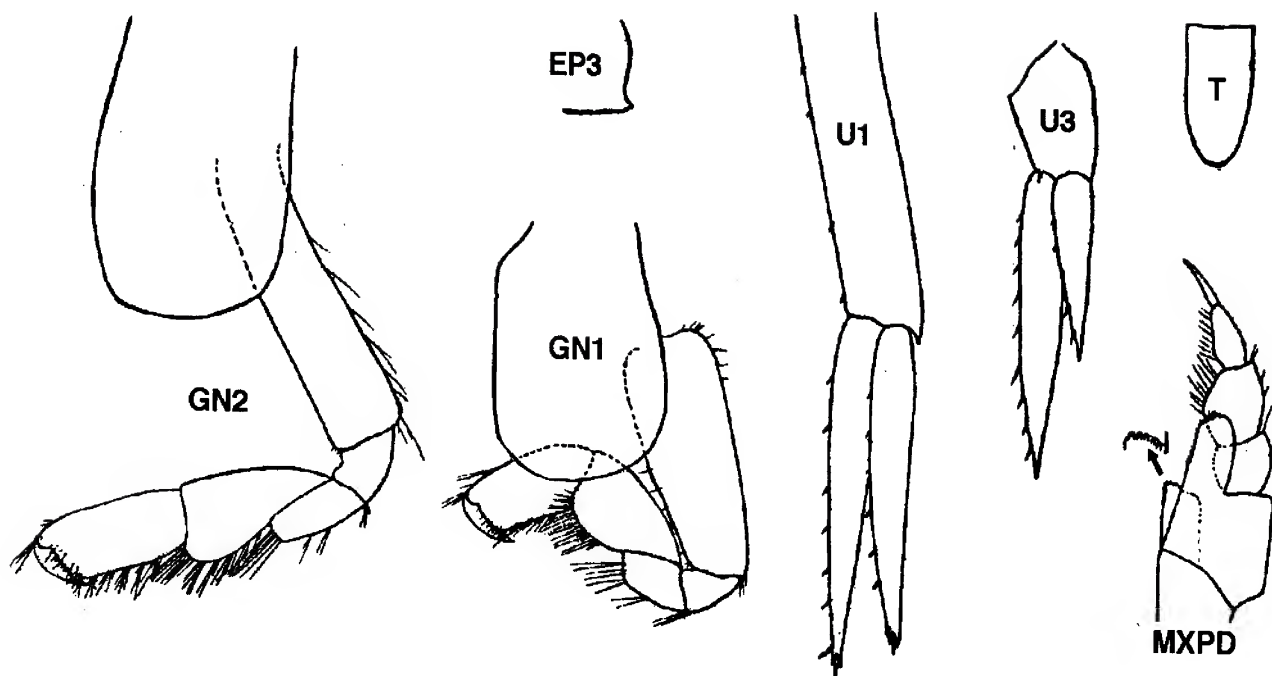


FIG. 4. *Chromopleustes oculatus* (Holmes, 1908). Female (11.0 mm). Monterey Bay, California. (modified from Holmes, 1908)

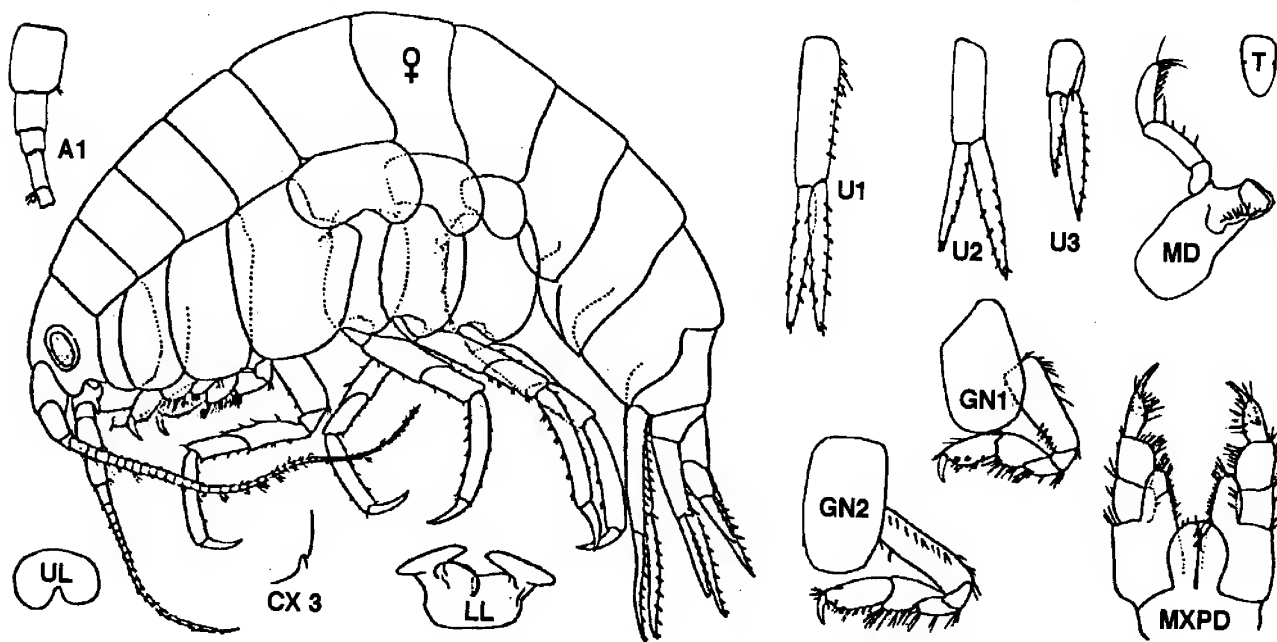


FIG. 5. *Chromopleustes* sp. 1. (Barnard & Given, 1960). Female (6.5 mm). Santa Monica Bay, 70 m. (after Barnard & Given, 1960)

Taxonomic commentary. The present female specimens compare closely with the 11.0 mm female illustrated by Holmes (1908) from Monterey Bay (Fig. 4). However, they differ from the small mature female illustrated by Barnard and Given (loc. cit.) from Santa Monica Bay, south of Point Conception, California (Fig. 5). The latter has relatively short antennal flagella, larger and broader coxal

plates 1-4, broader bases of pereopods 5-7, relatively weakly spinose uropod rami, relatively short telson, and much longer inner plate of the maxilliped. In order to clarify its taxonomic status, re-examination of the Santa Monica Bay material would seem desirable.

Chromopleustes oculatus displays a disruptive "saddle back" colour pattern, with dark vertical stripe and bright yel-

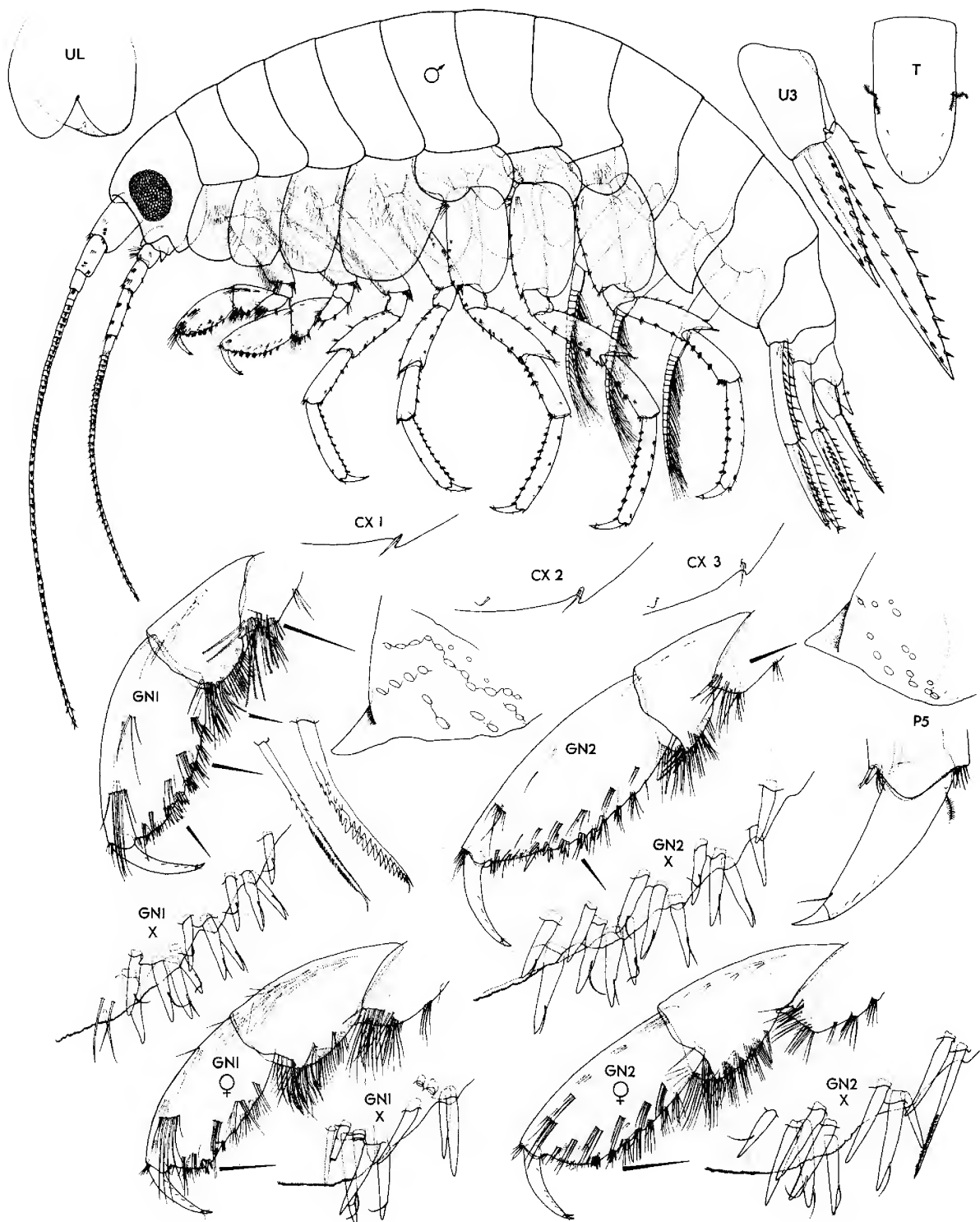


FIG. 6. *Chromopleustes oculatus* (Holmes) Male (8.2 mm); female ov (11.0 mm). Tongass Chan., Alaska

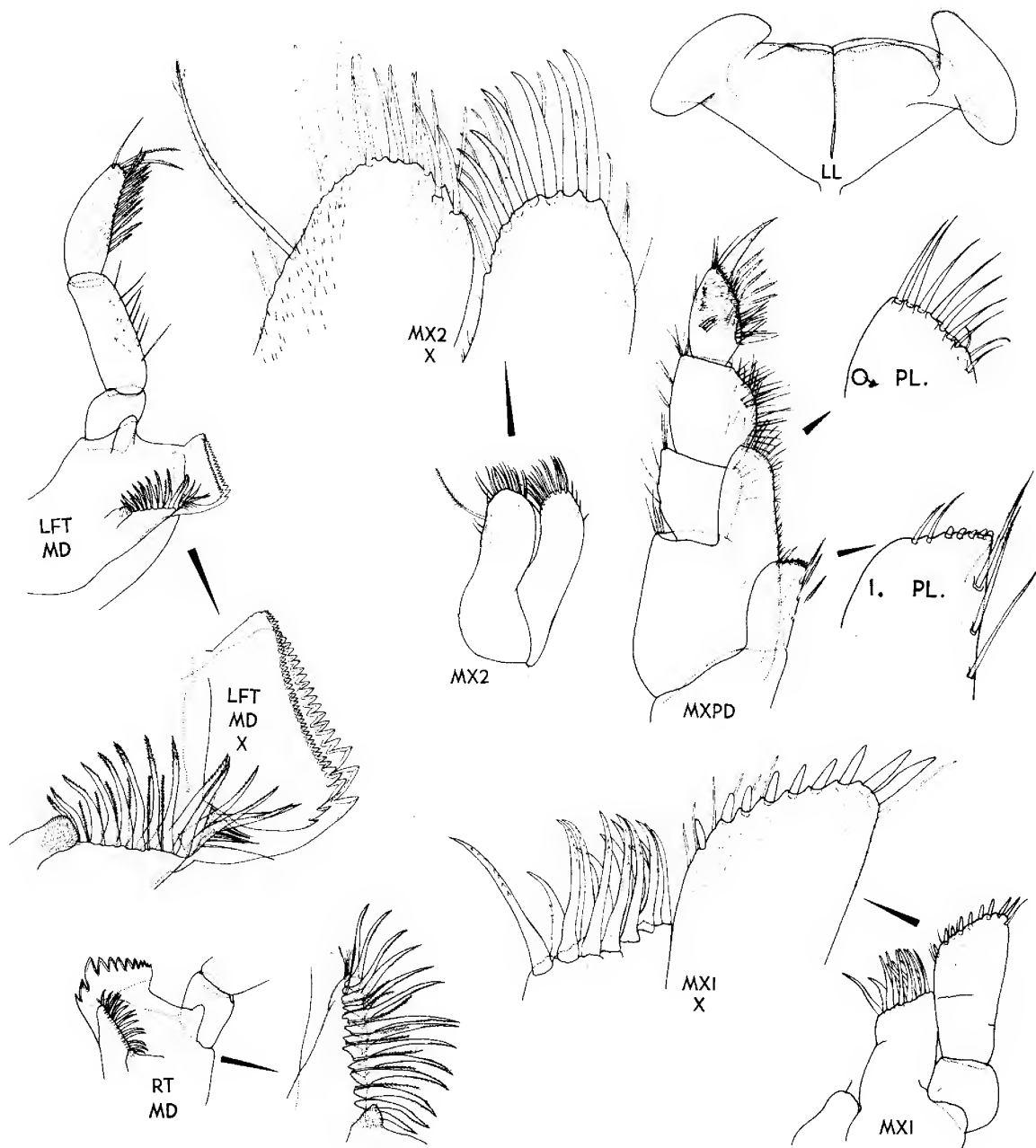


FIG. 7. *Chromopleustes oculatus* (Holmes). Male ov (8.2 mm). Tongass Channel, Alaska.

low spot on coxa 4 (see Bousfield, 1985, fig. 1), that is one of the most striking of all sublittoral North Pacific amphipods. The "saddle back" spot is wide, extending fully over the dorsum of pereopod segments 5 & 6, but only over segment 5 and half of segment 6 in *C. lineatus*. In *C. oculatus*, moreover, there are 3 dorso-lateral body stripes on each side, vs. 4-5 in *C. lineatus*, and coxal plates 1-3 are white, vs. brownish and vertically striped in *C. lineatus* (p. 81).

As noted elsewhere (Bousfield & Hendrycks, 1994), such may be a form of warning coloration, indicating the presence of terpenes or similar body chemicals that are distasteful to fishes and other potential predators.

***Chromopleustes johanseni* (Gurjanova)**
(Fig. 8)

Parapleustes johanseni Gurjanova, 1951: 550, fig. 446.

Parapleustes oculatus Barnard & Karaman, 1991: 650.—
Ishimaru, 1994: 54

Diagnosis. (after Gurjanova, 1951): Female (7.0 mm). Head, eyes relatively small, rounded, brownish, remote from the anterior margin by an eye width. Antenna 1 slightly shorter than antenna 2; flagellum 21-segmented. Antenna 2, flagellum 26-segmented.

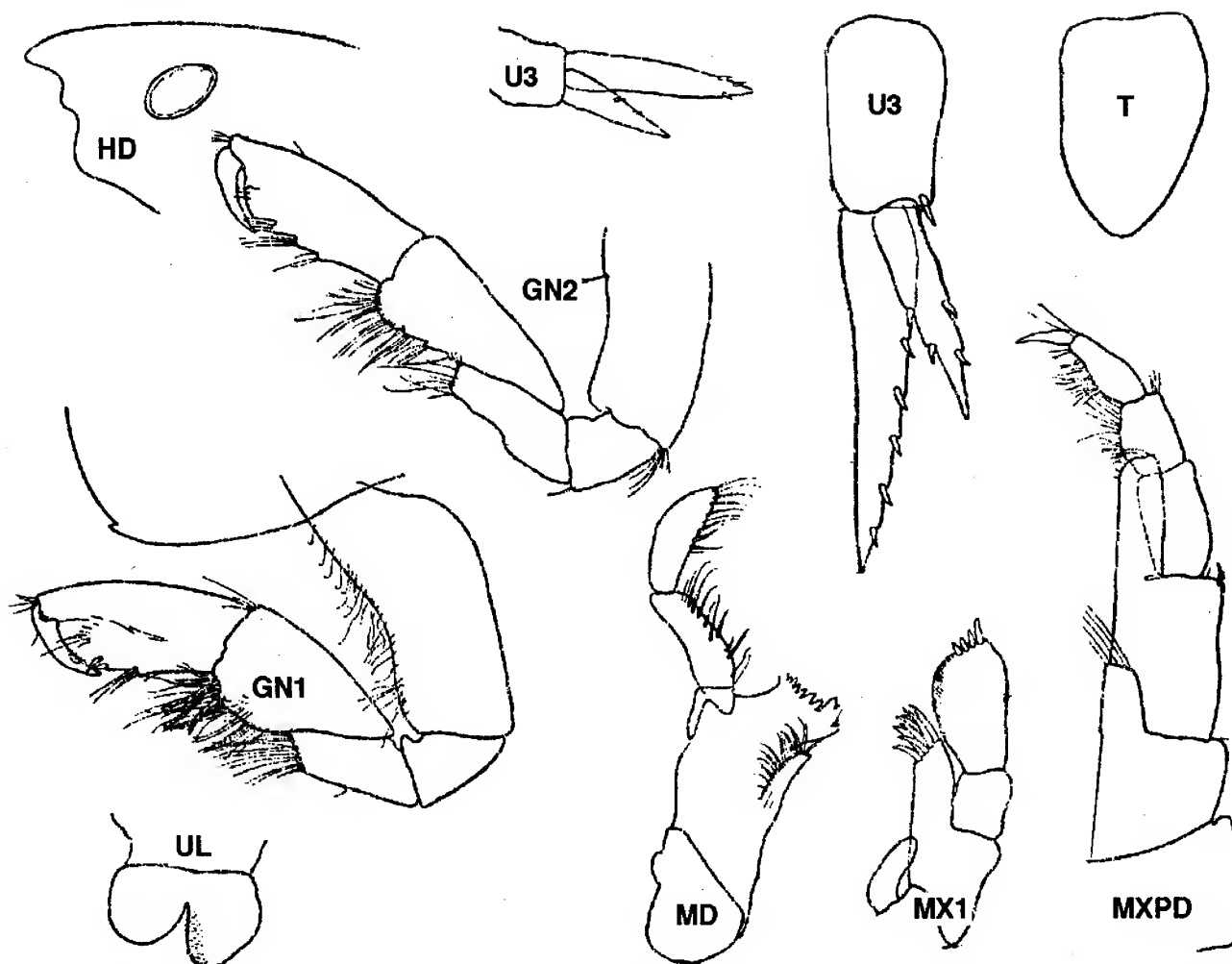


FIG. 8. *Chromopleustes johanseni* (Gurjanova). Female (7.0 mm). Bering Sea. (after Gurjanova, 1951).

Mandible, spine row with about 20 slender blades; right incisor, cutting edge with 12 teeth, largest proximally; palp segment 3 with 6-8 pectinate "D" spines. Maxilla 1, inner plate narrowly lobate, lacking apical seta; outer plate with 9 apical spines; palp segment 2 inner margin bulging inward, apex with 4 stout spines. Maxilliped, inner plate very short, apex setose; outer plate short, apex obliquely truncate; palp segments 1 and 3 longer than 2.

Gnathopods slender. Gnathopod 1, basis stout, heavy, posterior margin with strong proximal "hump", anterior margin richly setose; carpus large, longer than deep; propod more slender and a little longer than carpus, length ~2X depth, palm short, convex, oblique, postero-distal angle with few spines. Gnathopod 2, carpus elongate, length > 2X depth, posterior lobe shallow; propod more slender, slightly shorter than carpus, palm convex and more oblique than in gnathopod 1.

Peraeopods 5-7 homopodous, bases broad. Uropod 3, inner ramus narrowly lanceolate, length ~2X peduncle, with 5-6 marginal spines; outer ramus short ~60% of outer ramus, with a few marginal spines distally.

Telson relatively short, length ~1.5 X width, apex broadly acute.

Distribution. Bering Sea and coast of Kamchatka, subtidally on *Alaria fistulosa*. Strictly Asiatic Pacific.

Taxonomic commentary. The species is plesiomorphic in most character states but is distinct in the weakly spinose rami of uropod 3, and very broadened palp of maxilla 1.

Chromopleustes lineatus, new species
(Figs. 9, 10)

Parapleustes oculatus Bousfield, 1985, part.

Material Examined. About 25 specimens in 10 lots:
ALASKA.

Southeastern Alaska: ELB Stn. A171 (Puffin Bay, Baranof I.), rock and algae at LW level, July 25, 1961 - 22 im.; ELB Stns., July, 1980: S7B1 (Dry Pass, Chichagof I.), under boulders, algae, LW - 1 female; S11B1 (Column Pt., Lisianski Strait), bedrock and kelp at LW, July 30, 1980 - ~50 specimens including males and females.

BRITISH COLUMBIA.

North-central coast: ELB Stn. N1 (Rivers Inlet), bedrock,

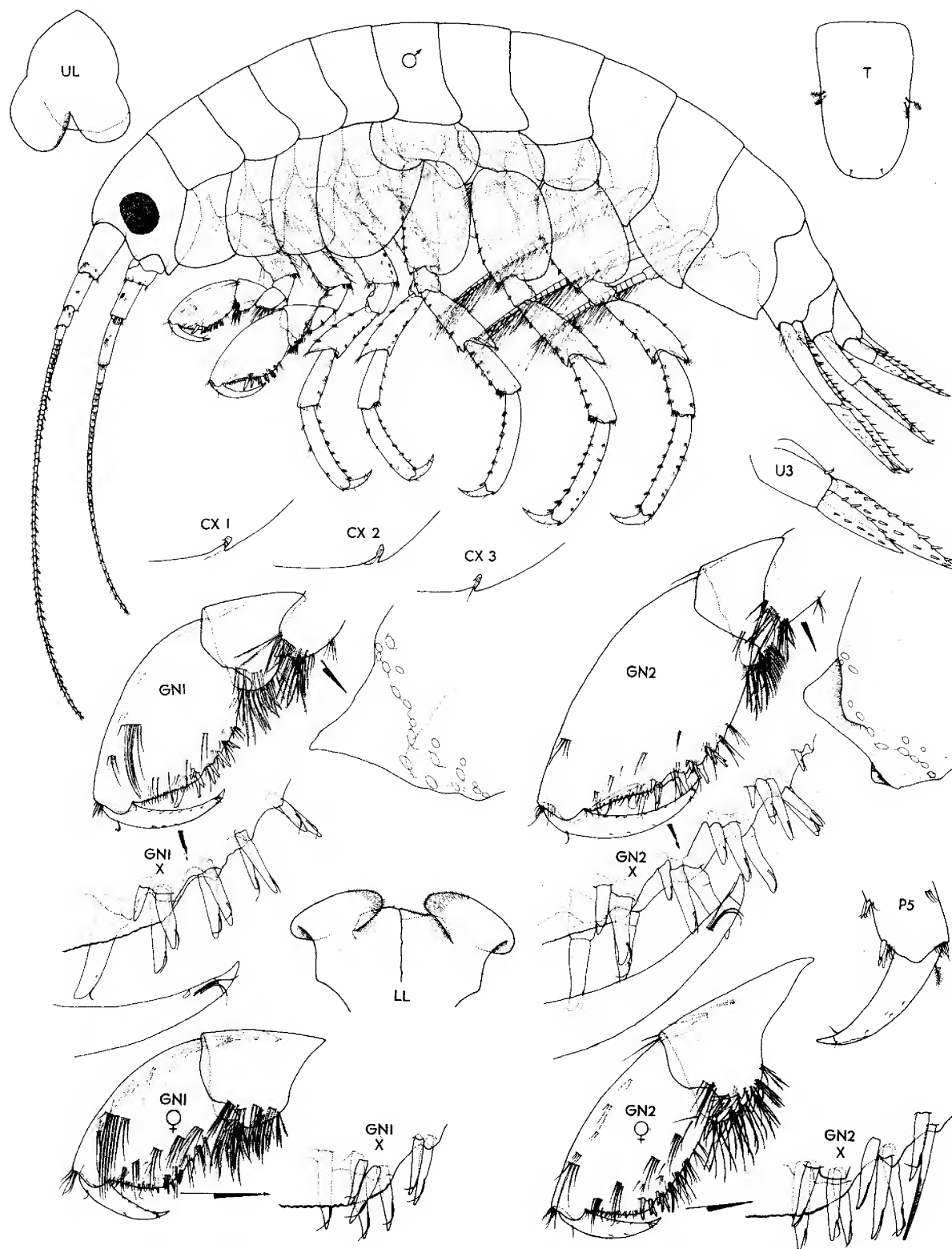


FIG. 9. *Chromopleustes lineatus*, new species. Male (7.5 mm); Female ov (9.0 mm) Ahous Bay, B. C.

Phyllospadix, and coarse sand at LW, Aug. 3, 1959 - 25 specimens, including males, females, im.

Vancouver I., north end: ELB Stn. O5 (Ferrer Pt. beach), under bedrock and kelp at LW, July 20, 1959 - 6 males 2 females, 3 im.

Vancouver I., south end: ELB Stn. O12 (Ahous Bay, Vargas

I.), bedrock, *Phyllo-spadix*, sand, at LW, Aug. 18, 1959 - male (7.5 mm), **Holotype** (slide mount), CMN Cat. no. NMCC1995-0071; female ov (9.0 mm), **Allotype** (slide mount), CMN Cat. no. NMCC1995-0072; 7 males, 3 females, **Paratypes**, CMN Cat. No. NMCC1995-0073. ELB Stns., 1975: P5c (Taylor I. Trevor channel), from ascidians and

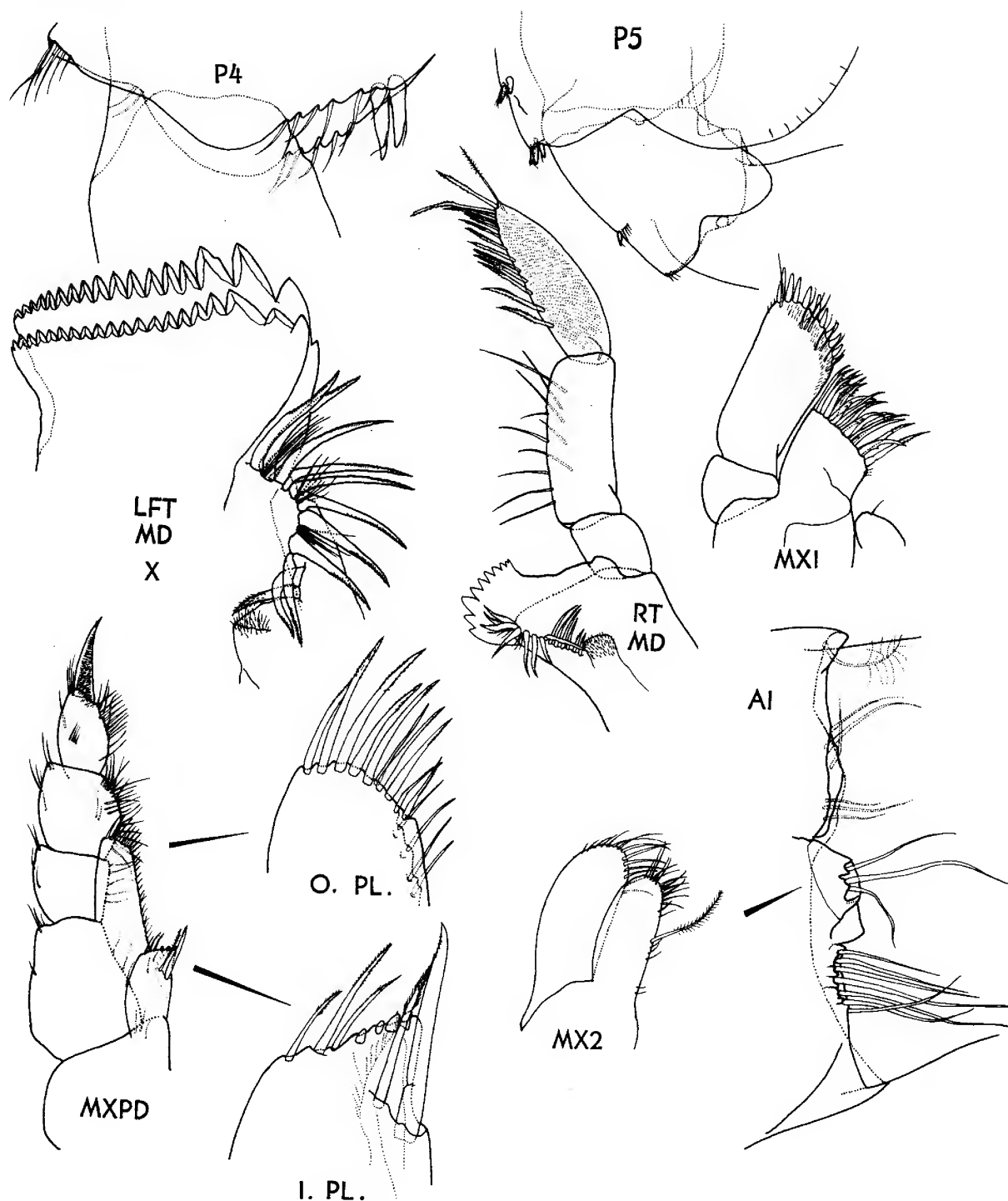


FIG. 10. *Chromopleustes lineatus*, new species. Male (7.5 mm); female ov (9.0 mm). Ahous Bay, B. C.

sponges under large boulders at LW level, - 1 male. ELB Stns., 1976: B7 (Broken Is., Trevor Channel), from sponges under rock, LW level - 9 males 6 females, 6 im. ELB Stns., 1977: B11b (Wickaninnish Bay, south end), from sponges and algae under steep bedrock walls at LW - 1 male, 2 females; B13 (Trevor channel, off Brady's beach), 6-14 m dredge, sand, stone, algae - 1 female ov (14 mm); B14 (Trevor channel, off Execution rock), 44-54 m dredge, sandy mud, algae - 1 female ov.

CALIFORNIA.

Albion Cove, Mendocino Co., from *Tealia* species, 20 m depth, T. Chess coll., Sept. 26, 1978 - 110 females, 20 males.

Diagnosis. Male (7.5 mm): Head, eye broadly ovate, black in alcohol. Antenna 1, flagellum ~60-segmented; accessory flagellum minutely subconical, with 3 apical setae. Antenna 2, peduncular segment 5 little longer than 4; flagellum ~35-segmented.

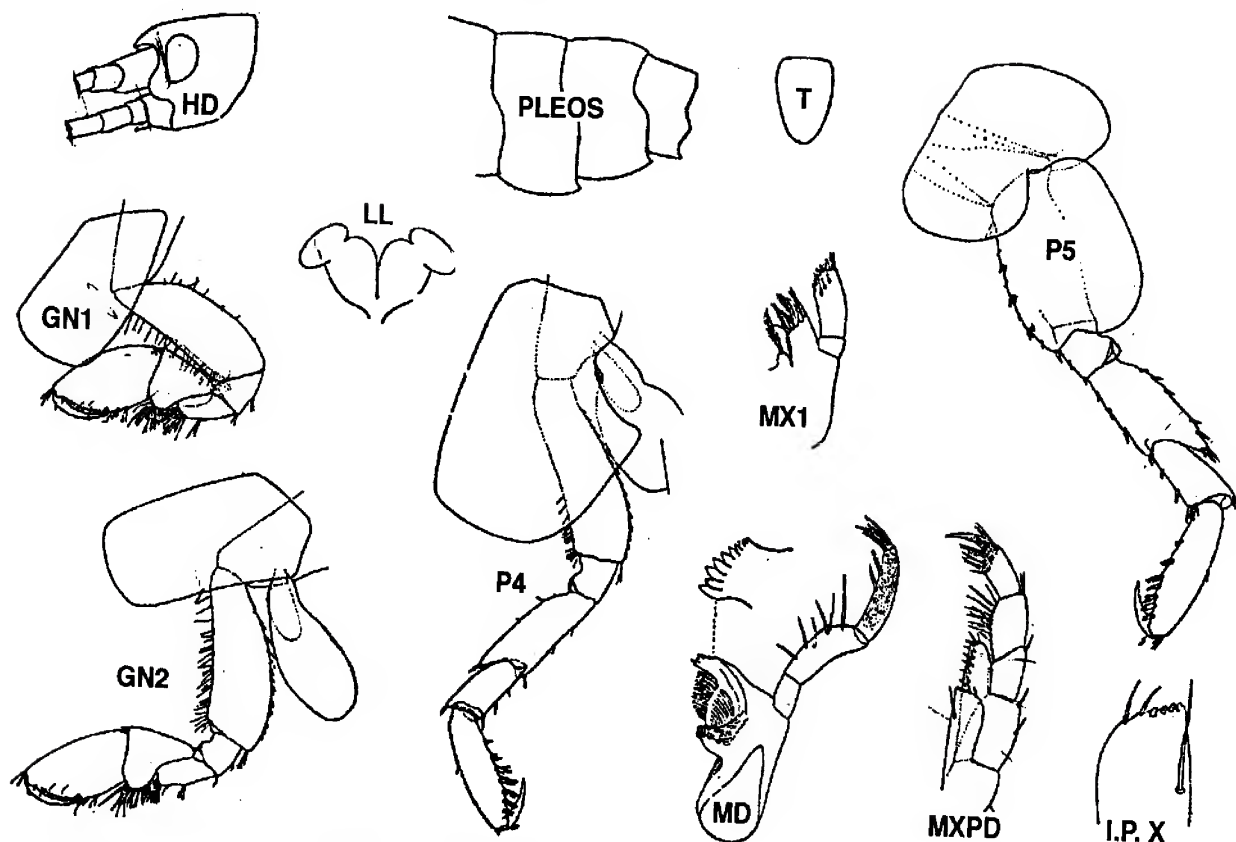


FIG. 11. *Commensipleustes commensalis* (Shoemaker). Female ov (5.5 mm). Point Barrow, Alaska. (after Shoemaker, 1952).

Upper lip with deep V-cleft separating asymmetrical lobes. Lower lip, inner lobes broad, flat. Mandible, spine row with 11-13 slender blades plus supernumerary setae; right incisor with 9, left incisor with 17 stout teeth; left lacinia with ~20 teeth, distally smallest; palp segment 3 with 10 pectinate "D" spines (of Cole, 1980) and 3 longer apical setae. Maxilla 1, inner plate with single short apical setae; outer plate with ~18 slender apical spines; palp segment 2 apically rounding, with 8-9 short spines. Maxilla 2, outer plate broader than inner. Maxilliped, inner plate with large inner marginal blade-like spine and 4 small apical denticles; outer plate rounded apically; palp segment 1 shorter than 2.

Coxae 1-3 relatively broad, deep. Gnathopods distinctly sexually dimorphic. Gnathopod 1, posterior margin of basis lacking distinct proximal "hump"; carpus short, as deep as long; propod relatively deep, length ~ 1.5 X depth, palm oblique, nearly straight, postero distal angle with 4 groups of spines extending onto posterior margin. Gnathopod 2, propod very short, length distinctly less than depth; propod larger than in gnathopod 1, slightly broadening distally, palm oblique nearly straight, posterior angle with 4 spine clusters and adjacent single small spine on posterior margin; dactyls with minute posterior marginal setules.

Peraeopods 3 & 4, segment 6 relatively short, hind margin with 6-7 spine clusters. Peraeopods 5-7 homopodous, peraeopods 5 slightly the shortest; basis of peraeopod 5 less broadly expanded than in 6 & 7; dactyls medium, gently curved distally.

Pleon side plate 3, hind corner acuminate; uropods 1 & 2 slightly shorter and less strong than in *C. oculatus*; inner ramus of uropod 1 with 6-8 serial paired spines. Uropod 2 Uropod 3, inner ramus, length ~2X peduncle, margins with 8-9 serially paired spines

Telson medium, length 1.5 X width, apex subtruncate.

Female (9.0 mm): Slightly larger and heavier-bodied than male. Gnathopod 1, carpus slightly longer, length slightly greater than depth; propod shorter, length ~ 1.3X depth. Gnathopod 2, carpus not shortened, length ~1.5 X depth; propod subrectangular, not broadening distally.

Distribution. From southeastern Alaska, through the Queen Charlotte islands and north central mainland coast of British Columbia to Mendocino Co., northern California, often in association with sponges, coelenterates and tunicates, on hard bottoms, from LW level in the north, subtidally to depths of over 50 m in the south.

Etymology. from the Latin "*lineus*": meaning lined, alluding to the fine, orange, dorso-lateral body stripes, and verical yellow stripes on brownish coxal plates 1-4.

Taxonomic commentary. The species differs markedly from *C. oculatus* in colour, and from *C. johanseni* in characters of the key (p. 74), and additionally in the highly modified mouthparts, especially the mandible and maxilla 1.

Commensipleustes, new genus

Parapleustes Shoemaker, 1952: 231.—J. L. Barnard, 1969a: (partim).—Barnard & Karaman, 1991: 650.

Type specis. *Parapleustes commensalis* Shoemaker, 1952: 231, fig. 83. (see Fig. 11).

Diagnosis. Head, rostrum about equal to rounded anterior lobe. Eyes medium large, black. Antennae slender, peduncles short, flagella short (<15 segmented).

Upper lip, medium notch shallow, lobes slightly asymmetrical. Lower lip inner lobes deep medium wide, rounded; outer lobes small, ovate, oblique. Mandible, molar process relatively strong, apex slightly tritulative(?); spine row with numerous (10+) blades; left lacinia 10-dentate; palp segment 3 slender, with 2 inner marginal pectinate "D" spines. Maxilla 1, inner plate small, with single apical seta; palp segment 1 lacking shoulder seta(e) segment 2 stout, apex obliquely rounded, with 8 short spines, and a facial row of 3 setae. Maxilla 2, inner plate regular, with single inner marginal plumose setae. Maxilliped, inner plate with 3 apical "button" spines and 2 slender spines; outer plate, apex with 2 slender spines, segment 3 lacking distal pectinations; palp relatively short, curved.

Coxae 1-3 relatively narrow, 1 not expanded distally. Lower margins gently convex, hind cusp minute. Coxa 4 not broader than deep. Gnathopods medium strong, closely subequal, not sexually dimorphic (?). Gnathopod 1, basis, anterior margin strongly short-setose; hind margin weakly so merus lacking distal process; carpus, hind lobe relatively broad, rounded below; propod relatively short, not expanding distally; palm oblique, convex, median tooth apparently lacking.

Peraeopod 3 & 4, basis, antero-distal margin with short setae; segment 5 short, length < segment 4; segment 6 stout, hind margin distally with groups of stout spines against which the dactyl closes, forming a grasping organ. Peraeopods 5-7 homopodous, short, stout; bases medium; segment 5 short; segment 6, anterior marginal spines and dactyl forming a grasping organ, as in peraeopods 3 & 4.

Pleon plates 2 & 3, hind corners mucronate, slightly produced. Uropods 1 & 2, relatively short, little or not exceeding uropod 3. Uropod 3, inner ramus relatively long.

Telson linguiform, medium, distally narrowing to rounded apex.

Distributional ecology. *Commensipleustes commensalis*, the only known species, occurs on pleopods of the spiny lobster, *Panulirus interruptus*, off Santa Barbara, CA. Also recorded by Wicksten (1982) off southern California.

Taxonomic commentary. The prehensile peraeopods, in combination with the short peraeopodal segment 5, unexpanded coxa 1, and specialized mouthparts are here deemed sufficient for separate generic recognition.

Gnathopleustes, new genus

Parapleustes Gurjanova, 1972: 131 (part).—Barnard, 1969b: 203 (part).—Barnard & Karaman, 1991: 649 (part).

Neopleustes Stebbing, 1906: 311 & 728 (part).

Parapleustinae, group 1 (part) Bousfield & Hendrycks, 1994: 42.

Type species. *Iphimedia pugettensis* Dana, 1853, original description.

Species. *Gnathopleustes serratus*, new species (= *Parapleustes pugettensis* Shoemaker, 1964); *G. den* (Barnard, 1969b); *G. pachychaetus*, new species; *G. trichodus*, new species; *G. simplex*, new species.

Diagnosis. Body smooth above. Head, rostrum shorter than bluntly rounded anterior lobe; inferior antennal sinus broadly incised. Eyes medium large, subrotund. Antennae well-developed; posterior margins often setose. Antenna 1 the longer, peduncular segment 2 short; accessory flagellum minute, apex 2-3 setose. Antenna 2, peduncle strong, flagellum often with special thickened setae.

Mouthparts strongly modified. UL shallowly notched, lobes asymmetrical. Lower lip broad, outer lobes rounded, oblique. Mandible: incisor regularly toothed; left lacinia 7-10 dentate; blades 4-12 in number, stout, distally chisel-shaped; molar body reduced, slender, apex fuzzy; palp normal, segment 1 short, segment 2 medially setose. Maxilla 1, outer plate with 9 tall slender apical spines; palp with subapical facial setae. Maxilla 2, inner plate little expanded; maxilliped, palp strongly dactylate, segment 2 largest; outer plate segment longer than palp segment 1, not enormously developed; inner plate short, inner marginal setae numerous (4-9).

Coxal plates wide, deeper than corresponding body plates; coxa 1 broadened distally, hind margin spinose near basis, postero-distal notch single, small. Gnathopods 1 & 2 large, subequal (Gnathopod 2 larger), variously sexually dimorphic; basis stout, with antero-distal setal group; merus with slight distal process; carpus, posterior lobe short, deep (especially in male); propods subovate, palms strongly oblique, elongate, convex, palmar tooth distinct, near hinge; palmar margin tending to be lined with special thickened or blade-like setae; postero-distal angle with 2-4 groups of spines, hind margin short, bare, or longer, setose.

Peraeopods 3-7 stout, spinose, normal; segment 5 strong, moderately overhung proximally by segment 4; dactyls medium strong, curved. Peraeopods 3 & 4, margins of segments 4, 5 & 6 may bear special thickened setae. Peraeopods 5-7 regularly homopodous, bases broad, convex behind.

Pleon side plates broad, deep, hind corners acuminate but not strongly produced. Pleopods strong, normal, not sexually dimorphic. Urosome short, segment 2 nearly occluded dorsally. Uropods 1 & 2 regularly spinose; uropod 1, rami

KEY TO KNOWN SPECIES OF *GNATHOPLEUSTES*

1. Antenna 2 about 10-15% shorter than A1, flagellum moderately to strongly setose posteriorly; gnathopods tending to strong sexual dimorphism, palmar margins heavily lined with blade-setae or split-tipped setae in male 2.
—Antenna 2 short, only 25-50% length of antenna 1, flagellum nearly bare (short setae only); gnathopods pods slightly sexually dimorphic, palmar margins lined with relatively few normal setae 5.
2. Gnathopods (male), palmar and posterior margins heavily lined with split-tipped setae; mandible, blade row of 10-12 unmodified blades; antenna 1 (male), flagellum brushy. *G. simplex*. (p. 87)
—Gnathopods (male), margins lined with "balloon" setae (pachychaete); mandible, blades (especially distally) modified; antennal setation weak, with no distinct "brush" (setose on hind margin only) 3.
3. Antennal peduncles spinose, lacking setae; peraeopods 3-7 all lacking marginal setae; gnathopod palms strongly setose, *G. den* (p. 85)
—Antenna peduncles spinose and setose (flagella of A2 variously setose); peraeopods 3-4 or 5-7 strongly setose behind; gnathopod palms strongly setose (with "balloon" setae) 4.
4. Gnathopod 2, palmar margin distinctly concave, postero-distal angle with 2 spine groups; peraeopods 5-7, hind margins of segments 4-6 with clusters of long brushlike setae (male); uropod 3, outer ramus with 6-9 marginal spines; antenna 1, peduncular segment 1 not elongate *G. trichodus* (p. 91)
—Gnathopod 2, palmar margin nearly straight, postero-distal angle with 3-4 spine clusters; peraeopods 5-7, hind margins of segments 4-6 with spine clusters only (lacking setae); uropod 3, margins of outer ramus with 5-7 spines only; antenna 1, peduncular segment 1 long *G. pachychaetus* (p. 87)
5. Gnathopods, dactyls smooth behind; telson less than twice as long as wide; peraeopods 5-7, segment 5 distinctly shorter than 4, strongly overhung posteriorly by segment 4 *G. pugettensis* (p. 83)
—Gnathopods, dactyls posteriorly finely serrate; telson elongate, at least twice as long as wide; peraeopods 5-7, segments 4 & 5 subequal in length, 5 normally overhung by 4 *G. serratus* (p. 91)

subequal; uropod 2, outer ramus the shorter. Uropod 3, outer ramus distinctly the shorter. Telson elongate, narrowing distally; dorsal penicillate setae about mid-point from base. Coxal gills large, broad.

Taxonomic commentary. Members of *Gnathopleustes* overlap to considerable degree with members of *Incisocallope*. However, the two genera are maintained as distinct units for the present because they can be keyed, and the distributions are discreet. Within *Gnathopleustes*, two main subgroups can be distinguished, as outlined in the key below. In the more advanced members (*G. pugettensis*, *G. den*, *G. simplex*) the gnathopods appear very slightly sexually dimorphic, and the mouthparts, peraeopods and uropods are apomorphic.

Distributional commentary. Members of the genus are restricted almost entirely to the Pacific coast of North America, from southeastern Alaska to southern California. *Gnathopleustes pugettensis* has been reported, but not confirmed, from Japanese waters by Irie & Nagata (1962).

Gnathopleustes pugettensis (Dana)
(Fig. 12, 13)

Iphimedia pugettensis Dana, 1853: 932, pl. 63, fig. 6.
Neopleustes pugettensis Stebbing, 1906: 728.

Parapleustes pugettensis Barnard, 1969b: 203.—Austin, 1985: 592.—Stade, 1987: 379.—Barnard & Karaman, 1991: 650.

non Incisocallope newportensis Barnard, 1959: 22.

non Parapleustes pugettensis Barnard & Given, 1960: 43.
—Ishimaru, 1984: 19.

Material examined. 258 specimens in 38 lots:

ALASKA.

Southeastern Alaska. ELB Stns, June-July, 1961: A40 (4 + slide mount); A80 (1); A164 (1); A171 (1).

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns., July-August, 1957: W11 (6) W15b (1).

North-central coast, ELB Stns., July, 1964: H43 (1); H53 (1); W64 (2).

Northern and central Vancouver I.: ELB Stns., 1959: H10 (40 specimens including males and females); N16 (1); V4b (Hope I., Roller Bay), under boulders, kelp, *Phyllospadix*, at LW level - male (slide mount) (**fig'd specimen**); female (slide mount) (**fig'd specimen**) + 8 other specimens; V10(10); V17 (1); V19 (1).

Southern Vancouver I.: ELB Stns., 1955: P9(1). ELB Stns, 1970: P702 (20); P707 (5); P710b (1); P714 (1); P719 (5, including females ov.). ELB Stns, 1975: P2 (25); P3a (1); P5a (1); P5b (1). ELB Stn. B4, off Brady's Beach, 60-70 m

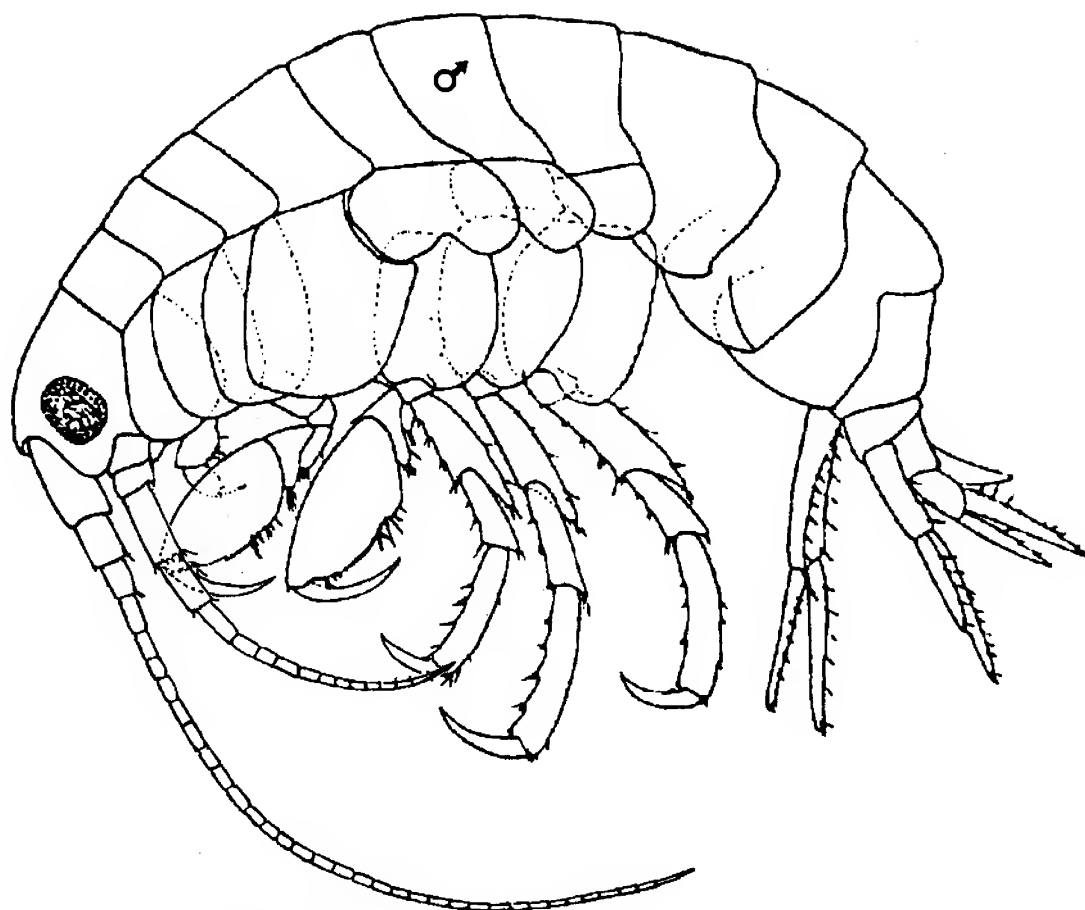


FIG. 12. *Gnathopleustes pugettensis* (Dana). Male (4.0 mm). Southern California. (modified from Barnard & Given (1960).

naturalist's dredge, sand and algae, June 25, 1976 - 2 females. ELB Stns., 1977: B8 (5); B14 (1).

WASHINGTON-OREGON:

Strait of Juan de Fuca to Newport. ELB Stns., July-Aug., 1966: W22 (30, including slide mount); W30 (1); W34 (11); W35 (9); W36 (8); W40 (19); W50 (30, + slide mount); W53 (1); W57 (1); W63 (6); W66 (2).

Diagnosis. Male (6.0 mm): Body relatively short, coxal and pleon plates deep. Head, eye large, subrectangular. Antenna 1, peduncular segment 3 relatively long (1/2 segment 2); flagellum of 35-40 medium long segments; accessory flagellum conical, apex with single long seta. Antenna 2, peduncular segment 5 shorter than 4; flagellum with ~35 nearly marginally smooth segments.

Upper lip strong, asymmetrical. Lower lip, inner lobes deep; outer lobes normally oval, oblique. Mandible, molar short, blunt; spine row with 8-10 stout, abruptly acute blades; incisor, cutting edge with 6 uneven teeth; palp segment 3 with 8 inner marginal pectinate spines; left lacinia with 8 unequal teeth. Maxilla 1, palp segment 2 with 4 unequal apical spines. Maxilla 2, outer plate not narrowing distally, apex strongly setose. Maxilliped, inner plate relatively large, distally broad, with 7 distal facial setae, and 4

small apical marginal denticles; outer plate regular, apex subtruncate; palp, dactyl slender, curved.

Coxae 1-3 relatively large, deep; coxa 5 deep. Gnathopod 1, carpus medium, about as deep as long, carpal lobe medium; propod smoothly ovate, palmar margin convex, very oblique, postero-distal angle with groups of 4 and 3 spines and a single spine distally on posterior margin; dactyl, hind margin not serrated, with a few setules only. Gnathopod 2, carpus and dactyl slightly larger, but proportions and armature similar to that of gnathopod 1.

Peraeopods 3 & 4 relatively short, distal segments (4/6) weakly marginally spinose; dactyls medium, > 1/3 length of segment 6. Peraeopods 5-7 closely homopodous, 5 slightly smallest; bases broadly expanded, hind margins convex; distal segments (4-6) weakly marginal spinose, not setose; dactyl medium.

Pleon plates 1-3 deep, broad, hind corner of 3 squared. Urosome 2 occluded dorsally by 1 & 3. Uropods ordinary. Uropod 1, peduncular postero-distal spine strong. Uropod 2, outer ramus short, length ~2/3 inner ramus. Uropod 3 strong, inner ramus > 2 X peduncle, margins with 5 spines.

Telson subrectangular, length about 1.5X width, apex truncate.

Female (5.5 mm): Gnathopods not described, presumably slightly smaller and less setose than in male.

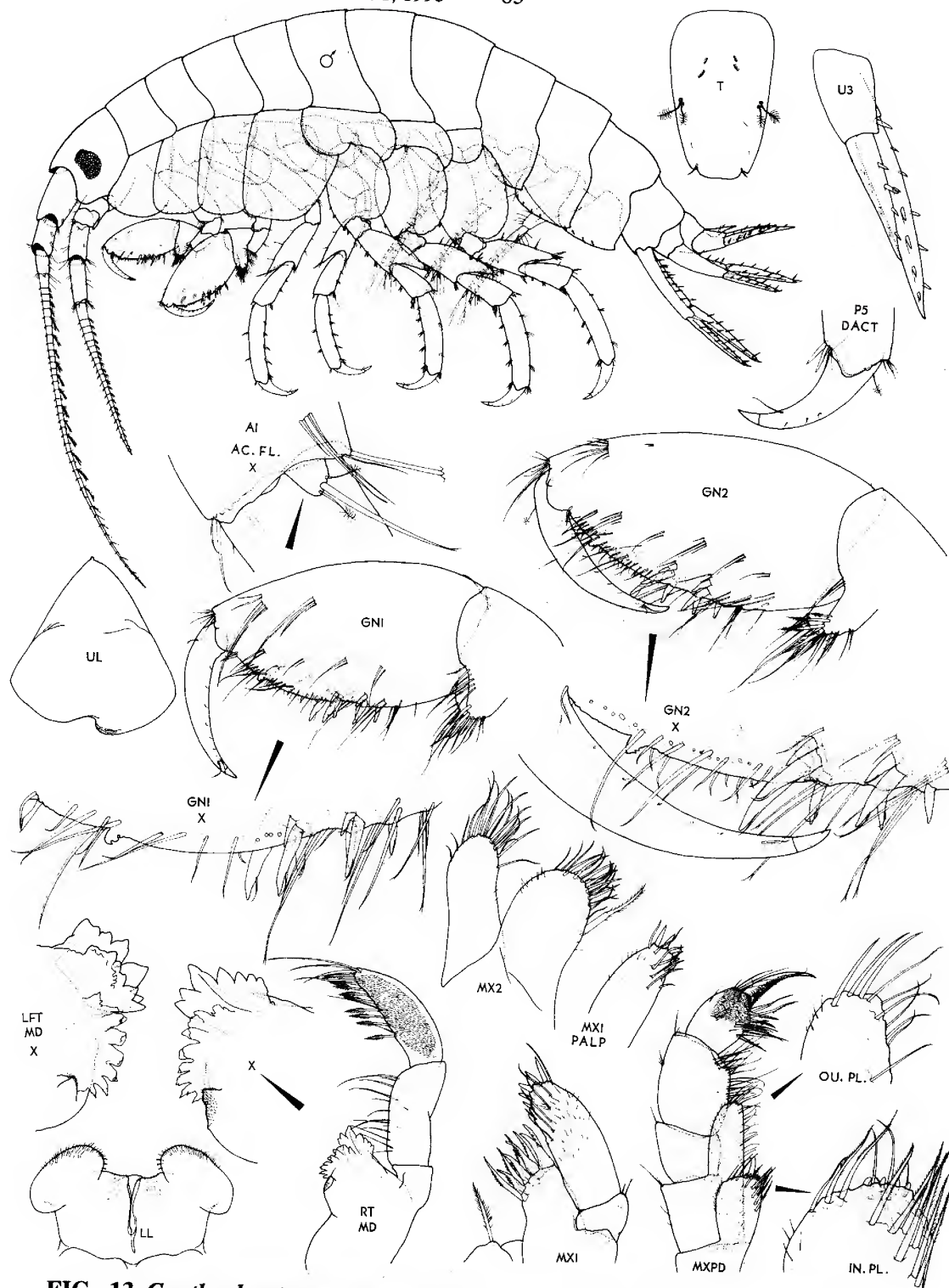


FIG. 13. *Gnathopleustes pugettensis* (Dana). Male (6.0 mm). Roller Bay, B. C.

Distribution. From southeastern Alaska and northern British Columbia south through Washington & Oregon to Point Conception and Santa Barbara regions, subtidally to 70 m; replaced by *I. newportensis* south of Pt. Conception.

Taxonomic commentary. *Gnathopleustes pugettensis* is the generic type and, in balance of character states, is most advanced. Overall, it is closely similar to *G. den* and *G. simplex*.

***Gnathopleustes den* (Barnard)
(Fig. 14)**

Parapleustes den J. L. Barnard, 1969b: 199, fig. 54.—
Staude, 1987: 319.—Barnard & Karaman, 1991: 650.

Material examined. Male (8.0 mm), **Holotype**, J. L. Barnard Stn. 6, Allan Hancock Foundation Cat No. #559. Material of this species was not found in the study range,

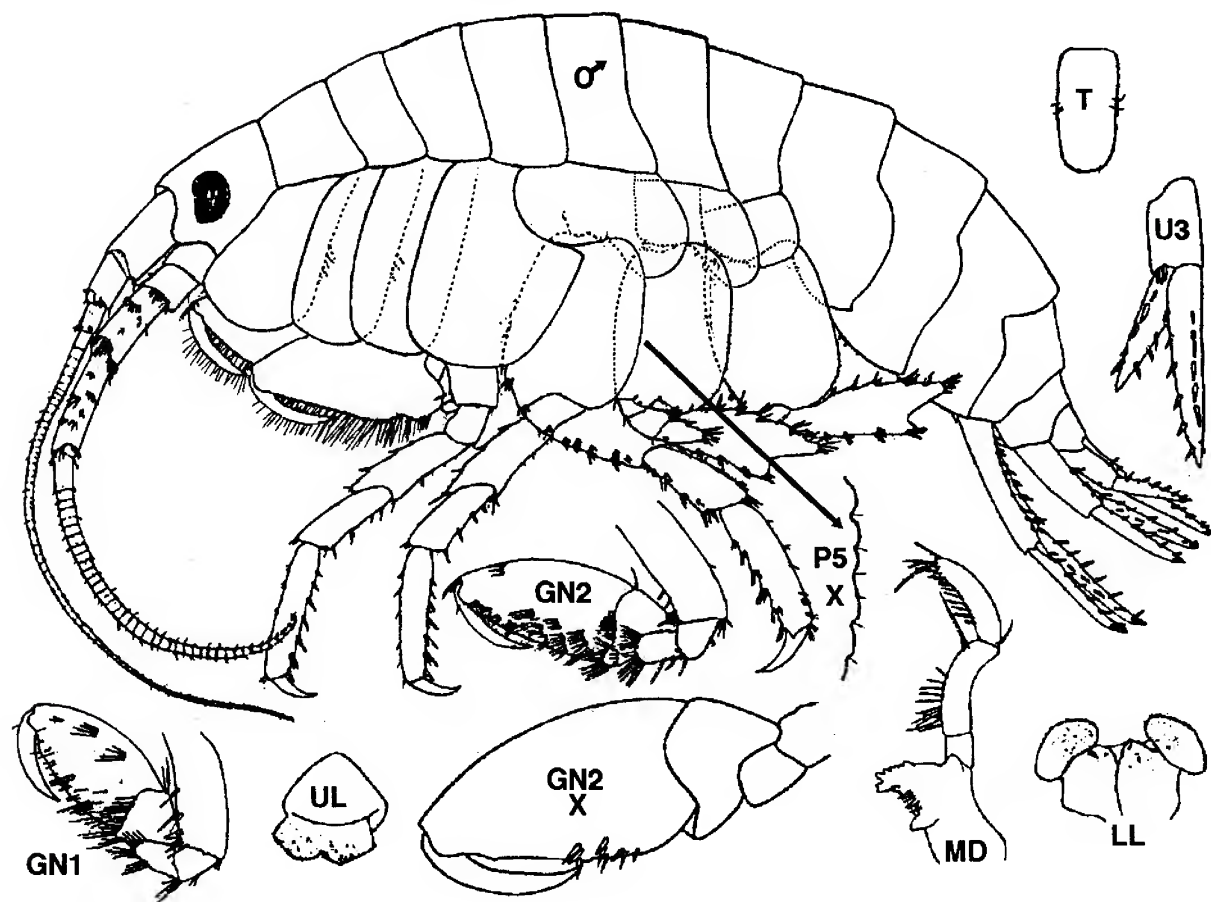


FIG. 14. *Gnathopleustes den* (J. L. Barnard). Male (8.0 mm). Corona del Mar, California. (after Barnard, 1969b).

despite its close similarity to *G. pachychaetus*.

Diagnosis (partly after Barnard 1969b). Male (8.0 m): Body and coxal plates medium, ordinary. Head, eyes medium, broadly short-reniform. Antenna 1, peduncular segment 3 medium, length 1/2 segment 2; accessory flagellum very short, with 2 slender apical spines; flagellum elongate (59 segments). Antenna 2, peduncular segment 5 not shorter than 4; flagellum with 50+ segments, proximally stoutest, nearly bare.

Upper lip, apical cleft relatively deep, lobes nearly symmetrical. Lower lip, inner lobes deep, outer lobes steeply oblique. Mandible, molar prominent, apex subacute?; spine row with 13-15 medium stout blades; left lacinia 9-dentate; cutting edge of incisor with 6 irregular teeth; palp segment 3 with 11-12 inner marginal pectinate "D" spines. Maxilla 1, palp, apex with 6-7 spines. Maxilliped, inner plate with 1 marginal spines and 2 facial setae; outer plate tall, columnar.

Coxal plates 1-3 large, deep, relatively narrow; coxae 1 distally expanding, 1-3 with 3-4 hind marginal spines; coxa 5, lobes medium deep. Gnathopod 1, carpus medium, length and depth subequal; propod ovate, palmar margin shallowly oblique, very slightly convex, densely finely setose, continuous with hind margin, median tooth very weakly developed; postero-distal angle with 3 groups of spines (?);

dactyl stout, hind margin smooth, not serrated. Gnathopod 2, propod distinctly larger and deeper than in gnathopod 2; palm nearly horizontal, nearly straight, densely finely setose, with weak median tooth, postero-distal angle with 3 groups of spines, a single distal spine on the posterior margin; dactyl stout, smooth behind.

Peraeopods 3 & 4 strong; segment 6, hind margin with 6 spine groups; dactyl short. Peraeopods 5-7 relatively stout; bases slightly broadest distally, hind margins nearly straight, weakly crenulate; segment 4 broad, width ~2/3 length; segment 6, margins spinose (not setose); dactyls medium, ~1/3 length of segment 6.

Pleon plate 3, hind corner acuminate. Urosome 2 with free dorsal margin. Uropods 1 & 2 stout, rami relatively short, not extending beyond uropod 3; uropod 2, rami subequal. Uropod 3, inner ramus with 6-7 pairs of marginal setae.

Telson subrectangular, length ~ 2X width, apex subtruncate.

Female (10.0 mm): Undescribed.

Distribution. Known only from the type locality at Corona del Mar, south of Pt. Conception, California, in washes of tubes of the polychaete *Phragmatopoma* sp., at LW level.

Taxonomic commentary. The type male specimen, figured by Barnard (1969b), differs from *G. pachychetus* in lacking posterior marginal setae on the peduncle of antenna 1, and in lacking brush setae on the flagellum of antenna 2.

Gnathopleustes simplex, new species
(Fig. 16)

Material examined.

BRITISH COLUMBIA:

Southern Vancouver Island: Off Wouwer I., Barkley Sound, P. Lambert coll., June 29, 1973 - male **Holotype** (6.8 mm) RBCM loan No. 973-156.

ELB Stn P17d, Kirby Pt. Bay, Diana I., under-rock habitat among sponges, tunicates, at LW, Aug. 6, 1975 - 1 female ov. (5.0 mm).

Diagnosis. Male (6.8 mm). Body slender coxal and pleonal plates relatively small, shallow. Head, eye medium small, broadly reniform. Antenna relatively short, 1 slightly longer than 2. Antenna 1, peduncular segment 3 short, length 1/2 segment 2; accessory flagellum minute, conical; flagellum with 35 segments, nearly devoid of marginal setae. Antenna 2, peduncular segments 4 & 5 short, 5 slightly longer, both with facial clusters of setae; flagellum of 30 weakly brush-like segments, basally stoutest, each with distal cluster of short setae.

Mandible, molar small apically conical; spine row with 10-11 slender blades and a few supernumerary setae; cutting edge of incisor with 6 variably sized teeth; palp segment 3 short, inner margin with 11 pectinate "D" spines; left lacinia with 12(?) teeth. Maxilla 1, palp slender with 4 apical slender spines? Maxilla 2? Maxilliped, inner plate short, broadest medially, with distal facial setae, and 4? apical marginal spinules; outer plate relatively short, distally narrowing, apex rounded; palp, dactyl curved.

Coxae 1-4 medium, 1 & 2 each with 2-3 posterior marginal spines. Gnathopod 1, basis with antero-distal marginal setae; carpus short, deeper than long, hind lobe distally broad; propod short ovate, relatively deep, palmar margin shallowly oblique, nearly straight, moderately marginally simple-setose, with distinct median tooth, postero-distal angle with cluster of 3 spines, posterior margin with single distal cluster of 2 spines; dactyl smooth behind. Gnathopod 2 similar, but large; basis with fewer antero-distal setae; carpus, hind lobe slightly broader; propod more elongate, palmar margin slightly concave; postero-distal angle with cluster of 3 spines; hind margin strongly setose, with distal cluster of 3 spines; dactyl smooth behind.

Peraeopods 3 & 4 ordinary, not setose; dactyls medium. Peraeopods 5-7 bases not strongly broadened, hind margins nearly straight; segment 4 short; segments 4-6 anterior and posterior strongly spinose and setose; segment 6, anterior margin with 6-7 clusters of spines and setae; dactyls medium.

Pleon plate 3 weakly spinose below, hind corner acuminate. Urosome 2 occluded dorsally by segments 1 & 3. Uropod 1, rami not elongate, weakly spinose marginally.

Uropod 2, outer ramus distinctly the shorter. Uropod 3 regular(?). Telson medium, narrowing distally 7 to sharply rounded apex.

Distribution. Known only from Barkley Sound, Vancouver I., British Columbia, LW and shallow subtidally, associated with sponges and tunicate, under rocks.

Etymology. From the Latin "simplex", meaning simple, not ornate, with reference to the unshortened, unbroadened blades of the mandibular spine row.

Taxonomic commentary. *Gnathopleustes simplex* encompasses some plesiomorphic character states (e.g., slender mandibular blades) but, in balance of character states, is apomorphic. It appears not unlike *G. pugettensis* and the more southerly *G. den*, in the form of the antenna and other features of the mouthparts, especially the maxilliped.

Gnathopleustes pachychaetus, new species
(Figs. 17,18)

Material examined.

ALASKA.

Southeastern Alaska. ELB Stns., June-July, 1961: A6 (1); A8(4 + slide mount); A130 (4); A171 28 + slide mount). ELB Stns, July, 1980: S4B4 (2); S11B1 (2); S18B1 (1); S22F1 (1).

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns., July-August, 1957: E21 (3); W9 (4). Flamingo Harbour, Stn. 3539, July 17, 1935 - 4 females ov; JFRB Stn. M1-65-55, DBQ, JWS coll., Aug. 6, 1965 - 1 female ov.

North-central coast, ELB Stns., July, 1964: H35 (~100); H39 (15); H40 (~70); H41 (~25).

Northern and central Vancouver I.: ELB Stns, July, 1959: O5 (~15); O17 (7); N18 (17, incl. males and females). R. M. O'Clair Stns, 1976: #760007, Kelsey Bay (1 male; # 760023, Squirrel Cove, Cortez I. - 30 males and female (+ slide mount); #760046, Port Hardy - 1 female ov.

Southern Vancouver I.: ELB Stns, July-August, 1955: P4 (~15); P6a (~40) P6c (~15); F5 (~15); M11 (~30). ELB Stns, 1970: P704 (1); P702 (1); P707 (~25); P708 (1). ELB Stns, 1975: P17d (1 female + slide mount); P5c (5); P20a (1); P20c (2). ELB Stns., 1976: B1 (10); B2 (6); B4 (9); B5 (44); B7 (2); B8 (1); B12b (~160 + slide mounts); B13 (~30) B28 (1). ELB Stns, 1977: B6a (3); B8 (1); B11a (1); B11b (2); B13 (1); B19b (2). R. M. O'Clair Stns., 1976: #760028, Sturdies Bay, Galiano I. - 9 males & females. # 760031 Miner's Bay, Mayne I. (~30 males, females). #760034, Horton Bay, Mayne I., June 22, 1976 - Male (6.8 mm), **Holotype** (slide mount), CMN Cat. no. NMCC1995-0076; female (5.8 mm), **Allotype** (slide mount), CMN Cat. no. NMCC1995-0077, + 8 males, 12 females, **Paratypes**, CMN Cat. no. NMCC1995-0078. Ogden Pt. breakwater, Victoria, R. J. Long coll., 1976 - 2 females, 1 male.

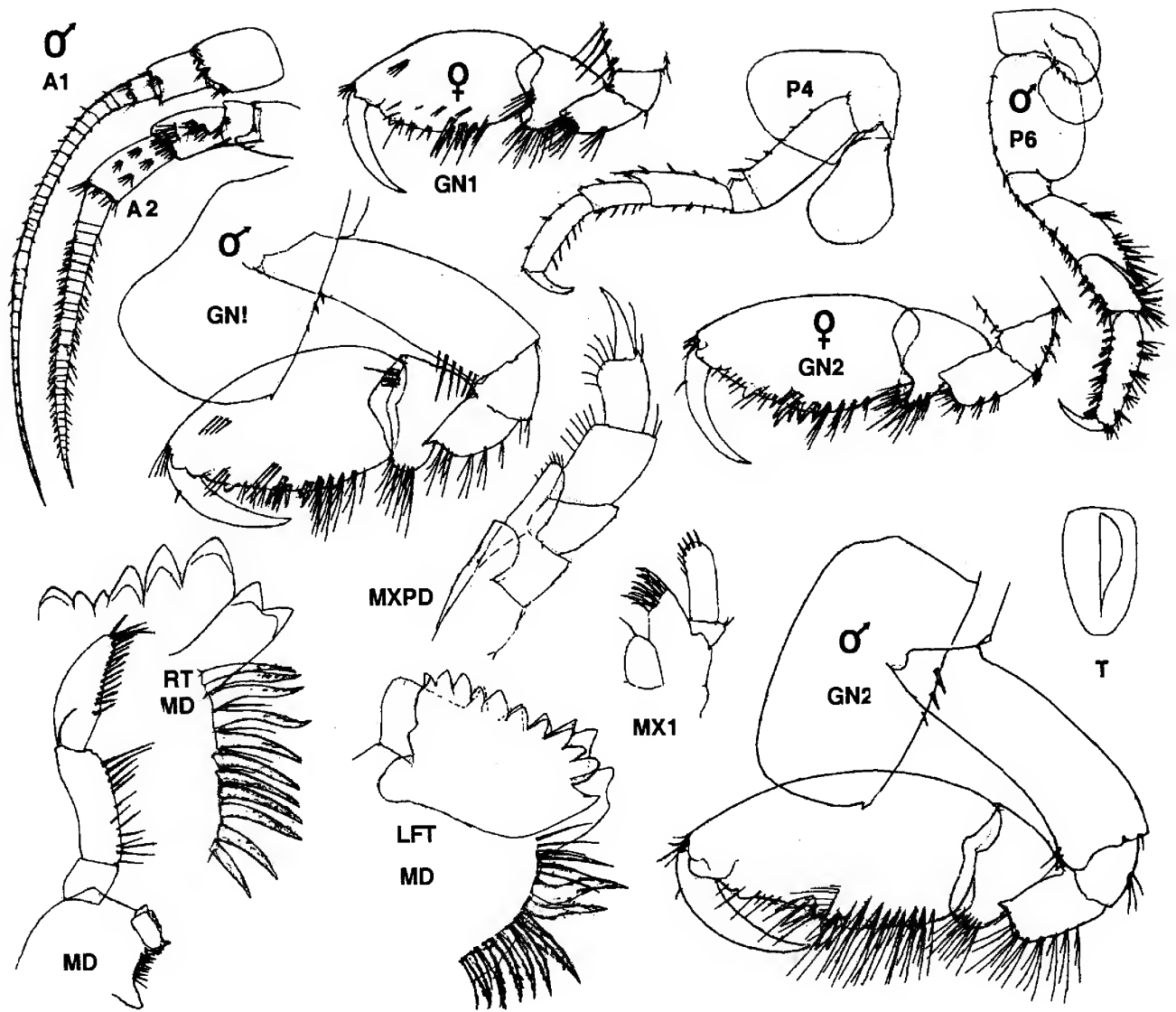


FIG. 16. *Gnathopleustes simplex*, n. sp. Male (6.8 mm); female ov (5.0 mm). Barkley Sound, B. C.

WASHINGTON-OREGON.

Coastal Stations, ELB, July-August, 1966: W2 (4 + slide mount); W5 (2); W22 (9 + slide mounts); W24 (~300); + slide mounts); W34 (15) W45 (9); W50(~50); W53 (10); W57 (~25); W58 (~28); W61 (23); W63 (~70).

Eagle Cove, San Juan I., R. M. O'Clair Stn. 74001, June 21, 1974 - 2 females (slide mount).

Charleston, Ore., mouth of Coos Bay, floating dock below LW, among *Enteromorpha* and *Polysiphonia* sp., K. E. Conlan coll., July 8, 1986: Stn 07-1 - ~70 males, females, im; Stn. 08-23 - 3 females, 4 im.

Diagnosis. Male (6.8 mm): Body slender, coxal and pleonal plates medium deep. Head, eye relatively small, short-reniform. Antenna 1, peduncular segments each with posterior marginal clusters of long setae; segment 3 long, length ~2/3 segment 2; accessory flagellum cone-like, with strong apical seta; flagellum with 48 segments. Antenna 2 shorter than 1; peduncular segment 5 not shorter than 4, both with

posterior and facial clusters of setae; flagellum relatively short, with ~40 short segments, brush-like posteriorly.

Upper lip tall, apical cleft shallow, lobes asymmetrical. Lower lip, inner lobes deep; outer lobes large, ovate, strongly oblique. Mandible, molar small apex subacute; spine row with 8-9 short thick blades, cutting edge of incisor with 7 regular teeth; palp segment 3 narrowing distally, inner margin with 18 pectinate "D" setae; left lacinia with 8-9-dentate. Maxilla 1, palp slightly narrowing distally, with 5 apical spines. Maxilla 2, outer plate narrowing distally apex relatively sparsely setose; inner plate with stout median marginal setae. Maxilliped, inner plate broad, with 7 distal facial setae and 5 apical marginal spinules; outer plate tall, columnar, apex rounded; palp segment 3 large stout, palp slender curved.

Coxal plates 1-3 each with single posterior marginal spine. Gnathopod 1, carpus shorter, deeper than long; propod ovate, narrowing distally, palm nearly horizontal with distinct median tooth, and dense clusters of long thick

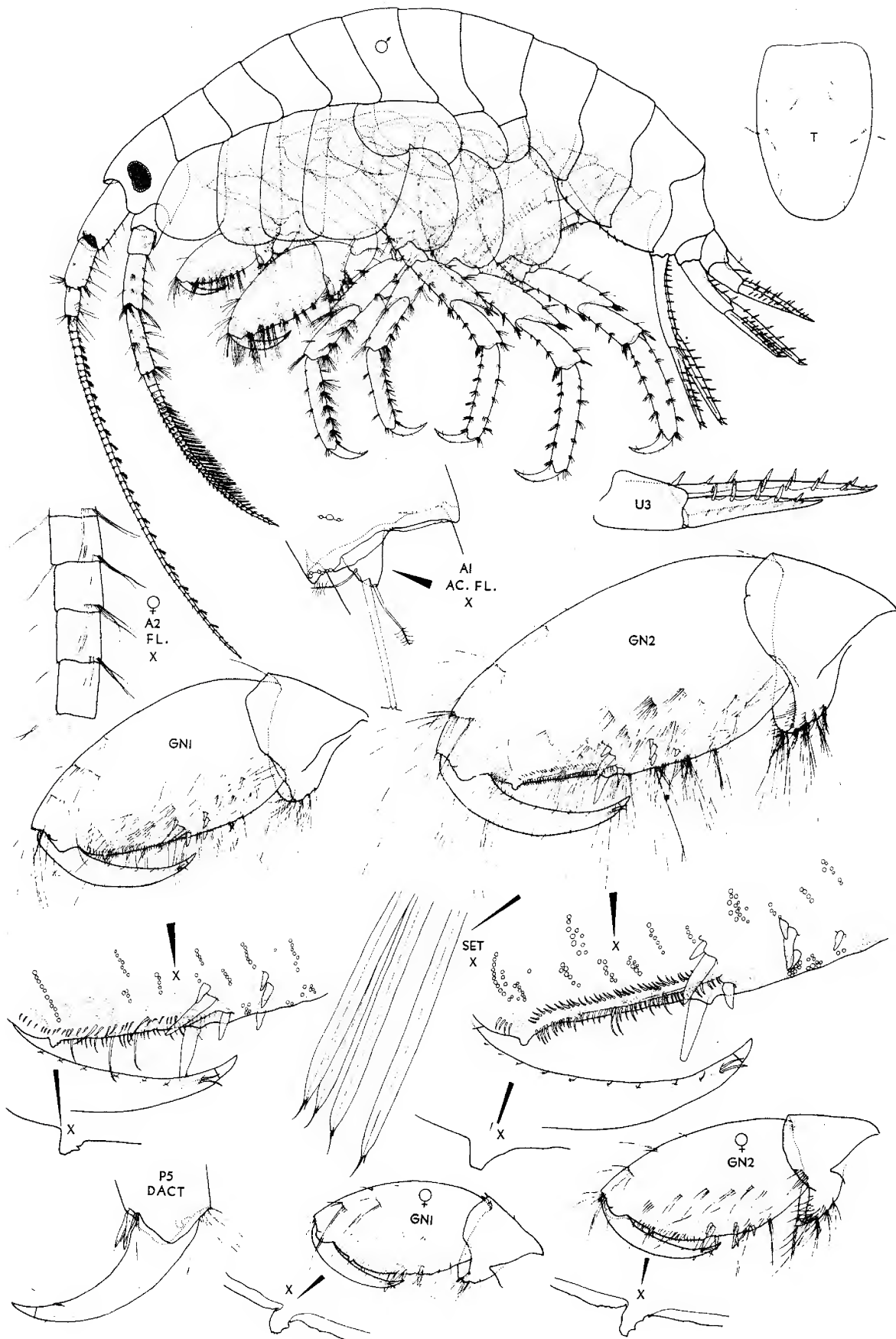


Fig. 17. *Gnathopleustes pachychaetus*, new species. Male (6.8 mm); female (5.8 mm). Mayne I., B. C.

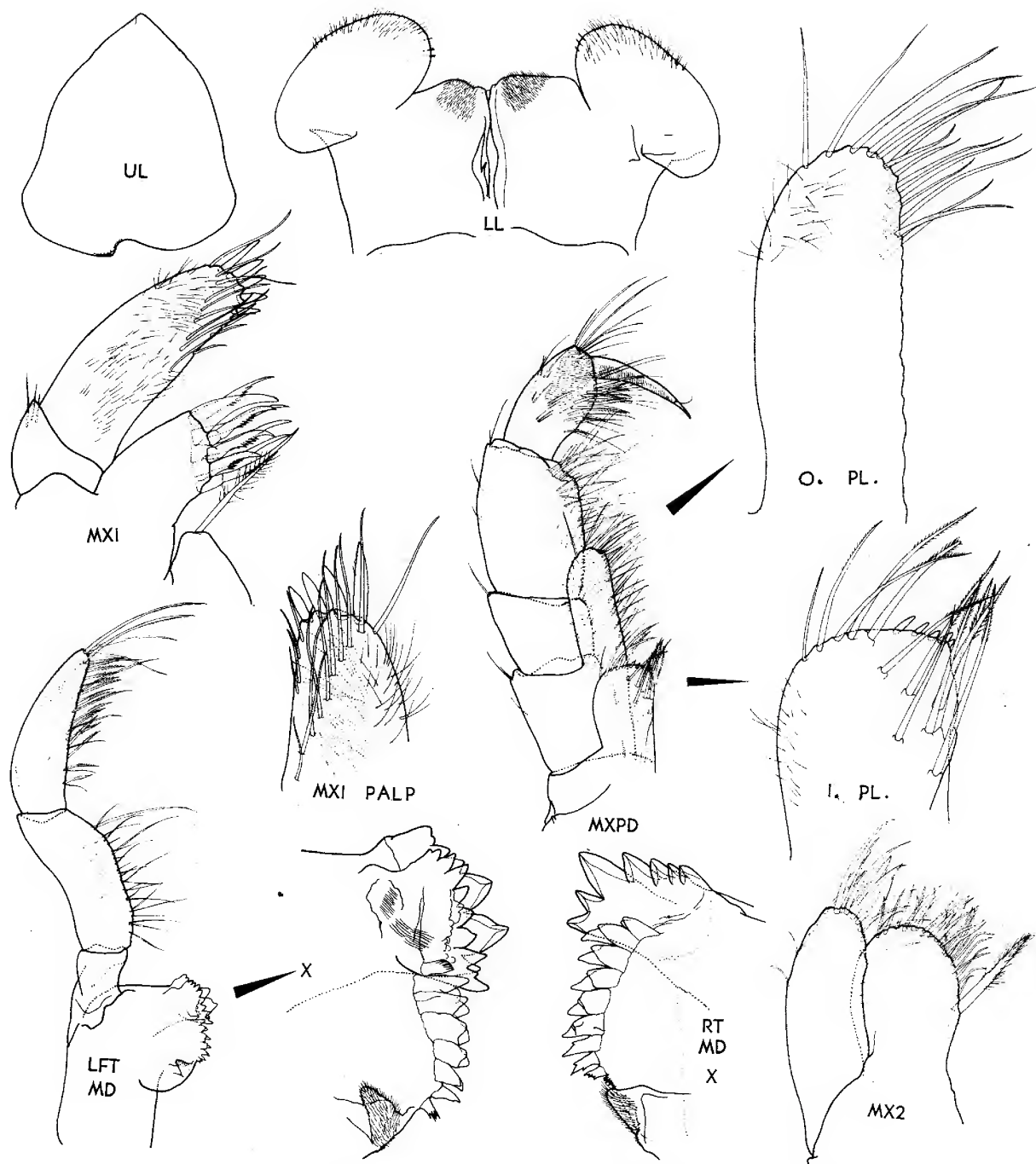


Fig. 18. *Gnathopleustes pachychaetus*, new species. Male (6.8 mm). Mayne I., B. C.

marginal "balloon" setae, margin merging smoothly with posterior margin, spine group at postero-distal angle with 4 spines, outermost largest, posterior margin with single distal cluster of 3 spines; dactyl, hind margin with a few small setules. Gnathopod 2 very similar but slightly larger, carpal lobe slightly deeper; palmar margin relatively short, distally slightly concave, postero-distal angle, spine cluster with 4 spines, posterior margin distally with a single spine and single cluster of spines.

Peraeopods 3 & 4, segment 4-6 with dense clusters of spines and setae especially posteriorly; dactyls medium. Peraeopods 5-7 similar, bases slightly broadening distally, hind margins gently convex; segment 5 short, segment 6

long, margins spinose, not setose; dactyls medium.

Pleon plates 2 and 3, lower margins weakly spinose, hind corners acuminate, slightly produced. Urosome 2 occluded dorsally by segments 1 & 3. uropods 1 & 2 slender, slightly exceeding uropod 3. Uropod 2, outer ramus distinctly shorter than inner ramus. Uropod 3, inner ramus with 6 pairs of marginal spines, outer ramus relatively large, = 3/4 inner ramus, margins 5-spinose

Telson broadly linguiform, apex broadly rounded.

Distribution. From southeastern Alaska, commonly throughout B. C. coastal waters, to southern Oregon, under rocks and among algae at LW level to shallow subtidal.

Etymology. From the Greek root words "*pachy*", meaning thick, and "*chaite*" meaning hair, in reference to the thick, broad, laminate setae comprising the setose armature of the gnathopods.

Taxonomic commentary. *Gnathopleustes pachychaetus* is somewhat similar to the more southerly species, *G. den*, in the strongly setose, weakly sexually dimorphic gnathopods, and in some mouthparts (e.g., mandibular blades). However, the gnathopod setae are more strongly thickened, and thick setae occur also on the distal segments of the pereopods, especially in the male. The posterior margins of peduncular segments of antenna 1 have 6-8 clusters of strong setae, and the flagellum of antenna 2 is brush-like, whereas corresponding parts of *G. den* are bare.

Gnathopleustes trichodus, new species
(Fig. 19)

Material Examined.

BRITISH COLUMBIA.

Southern Vancouver I.: West of Amphitrite Point, N. A. Powell Stn 67-83, 22 m, Aug. 22, 1967 - male **Holotype** (slide mount) CMN Cat. no. NMCC1995-0083.

Diagnosis. Male (8.5 mm): Body slender, coxal and pleonal plates medium deep. Head, eye broadly reniform, black. Antenna 1 shorter than antenna 2; peduncular segment 3 short, length < 1/3 segment 3; accessory flagellum conical, with 1 large apical setae; flagellum with 55 segments basally slightly short-setose. Antenna 2, peduncular segment 5 longer than 4, both with distal and facial clusters of setae; flagellum elongate, with ~50 segments, each with prominent distal whorl of short setae.

Upper lip, median notch shallow, lobes nearly symmetrical. Lower lip, inner lobes relatively shallow, outer lobes regularly ovate, oblique. Mandible, molar process prominent, apex subacute; spine row with 9 medium stout blades, tips obliquely acute; cutting edge of incisor with 6 irregular teeth; palp segment 3 slender, elongate, with 13 inner marginal pectinate "D" spines; left lacinia 9-10 dentate. Maxilla 1, palp slender, with 4 apical spines. Maxilla 2, outer plate distally narrowing, apex strongly setose. Maxilliped, inner plate short, with 7 distal facial setae and 5 apical marginal short spines; outer plate short narrowing to subtruncate apex; palp segment 3, inner margin with pectinate setae, dactyl slender, nearly straight.

Coxal plates 1-3 relatively broad, each with 1-3 hind marginal short spines. coxa 4 very broad, width and depth subequal. Coxa 5 shallow. Gnathopod 1, carpus short, deeper than long, lobe narrow; propod, palmar margin straight or slightly concave, median tooth strong, postero-distal angle with 2 groups of spines; median face with numerous clusters of slender thickened setae, giving densely setose appearance to propod; dactyl strong, not serrated behind. Gnathopod 2, similar, larger, very heavily setose; palm of

propod distinctly concave; dactyl stout, nearly smooth behind.

Pereopods 3 & 4, stout, margins of segment 4-6 setose and spinose; dactyls strong, >1/3 length of segment 6. Pereopods 5-7 subsimilar, bases regularly broadly ovate, smooth behind; segment 4-6 hind margins strongly setose and spinose; segment 4 relatively short; dactyls medium.

Pleon plate 3, lower margin weakly spinose, hind corner acuminate, slightly produced. Urosome 2 nearly occluded dorsally by segments 1 & 3. Uropods slender, elongate. Uropod 1, distal peduncular spine short. Uropod 2, outer ramus slightly shorter than inner ramus. Uropod 3 inner ramus slender, margins with 8 pairs of spines; inner ramus relatively long, with 5-6 pairs of marginal spines.

Telson linguiform, medium long, apex broadly rounded.

Distribution. Known only from the type locality near Amphitrite Pt., outer coast of southern Vancouver Island.

Etymology. From the Greek "*trichos*" mean hair, alluding to the dense setation of the gnathopods and pereopods.

Taxonomic commentary. *Gnathopleustes trichodus* is a primitive species, phyletically isolate from others of the group, especially in the form of the mouthparts, relative lengths of the antennae, broad coxal plates, concave gnathopod palms and densely setose pereopods.

Gnathopleustes serratus, new species
(Figs. 20, 21)

Parapleustes pugettensis Shoemaker, 1964: 410, fig. 10.

Material Examined. About 40 specimens in 15 lots: ALASKA. Southeastern Alaska. ELB Stns, 1961: A75 (Kayak, Wingham I.), LW, under boulders, June 27 - 5 males 3 females.

BRITISH COLUMBIA.

Queen Charlotte Island. ELB Stns, 1957: W12a(3); H11(1); Stn H14a, Yakan Pt., Graham I., under boulders at LW, Aug. 25 - male (8.7 mm), **Holotype** (slide mount) CMN Cat. no. NMCC1995-0068; female ov. (10.0 mm) **Allotype** (slide mount), CMN Cat. no. NMCC1995-0069; plus 10 males, 9 females, 1 im., **Paratypes**, CMN Cat. no. NMCC1995-0070. Northern Vancouver I.: ELB Stns N1 (Open Bight, Rivers Inlet)(5); V5 (Nigei I.) (2).

Southern Vancouver I.: ELB Stn. O15 (Box I, north end Wikaninnish Bay) (20); ELB Stn P719 (Cape Beale), 1970 - 1 male, 1 im. ELB Stn. B3 (Diana I., Trevor Channel), 1976 - 1 female. ELB Stn B6a (Trial I. Point, Victoria), 1977 - 4 specimens

WASHINGTON-OREGON.

ELB Stns, 1966: W40(4); W57(2); W58(4); W61(1); W63 (Cape Kiwanda) (>100).

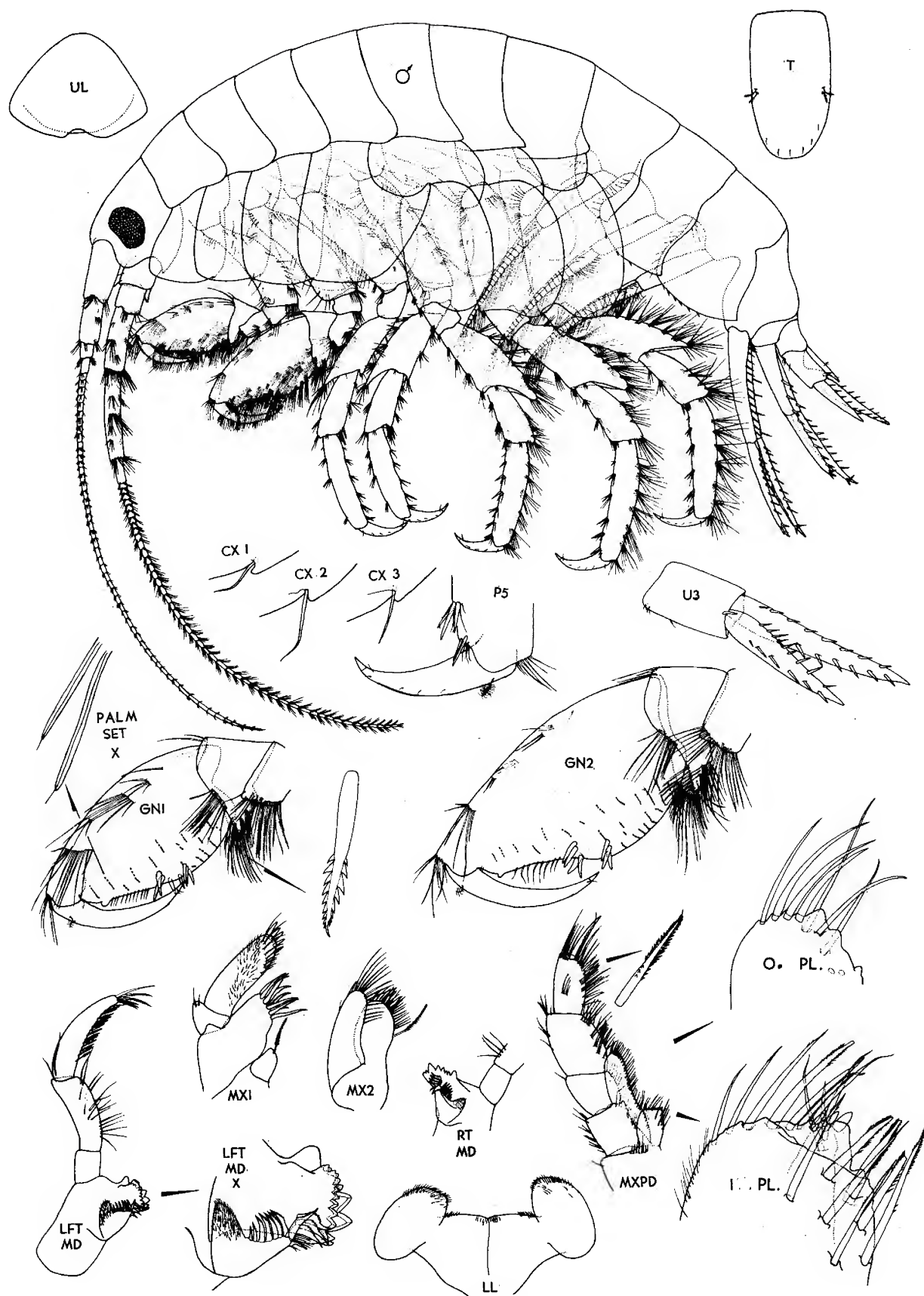


FIG. 19. *Gnathopleustes trichodus*, new species. Male (8.5 mm). West of Amphitrite Pt., V. I., B. C.

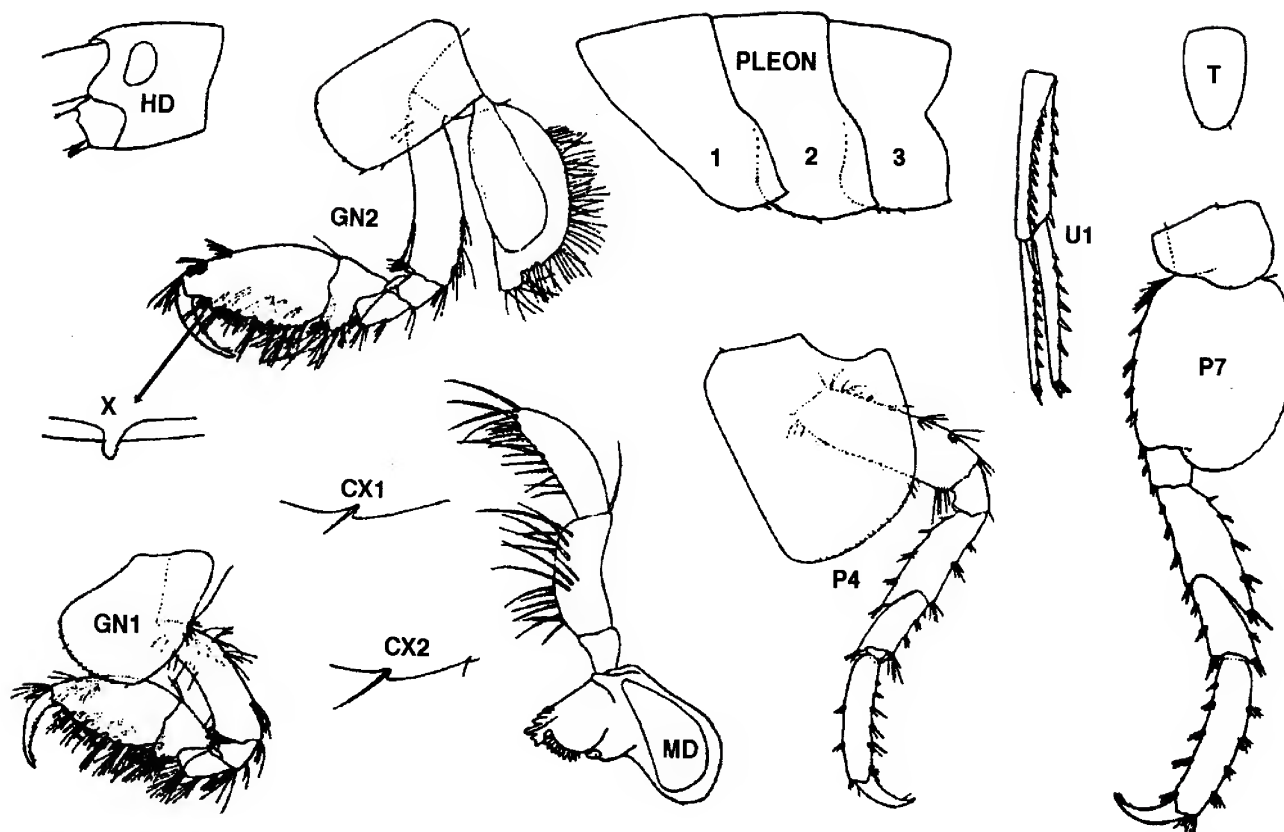


FIG. 20. *Gnathopleustes serratus* n. sp. Female (9.0 mm). Dillon Beach, CA. (after Shoemaker, 1964).

CALIFORNIA.

Albion Cove, at Cone Rock, Mendocino Co., Tony Chess coll., June 29, 1978 - 1 male.

Diagnosis. Male (8.7 mm): Body relative slender, coxal plates shallow. Head, eye large, subrhomboidal. Antenna 1, peduncular segment 3 medium; flagellum with ~45 short segments; accessory flagellum, truncate apex with 2 longish setae. Antenna 2, peduncular segment 5 not shorter than 4.; flagellum with ~25 segments, thickest proximally, each with distal ring of short "bottle-brush" setae.

Upper lip lobes distinctly asymmetrical. Lower lip, inner lobes deep, outer lobes short-ovate. Mandible, molar prominent, apex blunt; spine row with 8-10 thick, apically acute blades; incisor, cutting edge with 6 uneven teeth; left lacinia 8-dentate; palp segment 3 with 11-12 pectinate inner marginal "D" spines. Maxilla 1, palp stout, with 6 apical spines. Maxilla 2, outer plate not narrowing distally, apex strongly setose. Maxilliped, inner plate with 10 apical facial setae and 3 short apical spines; outer plate tall, distally narrowing; palp, dactyl slender, nearly straight.

Coxae 1 & 2, hind margin with 1-2 median short spines; coxa 4 shallow, broad. Gnathopod 1, carpus shorter than deep, hind lobe narrow; propod ovate, palm very oblique, gently convex, postero-distal angle with groups of 3 & 4 spines; dactyl strongly denticulate or serrated along proximal 2/3 of inner margin. Gnathopod 2, carpus short, hind lobe smaller than in gnathopod 1; propod long-ovate, very oblique

palm merging smoothly with hind margin, not heavily marginally setose; postero-distal angle with 2 groups of 4 spines; dactyl serrated behind.

Peraeopods 3 & 4, segments regularly spinose; segments 5, hind margin with 5 clusters of short spines; dactyls short. Peraeopods 5-7 closely homopodous, 5 slightly shortest; bases broadly expanded, hind margin strongly convex, minutely serrulate; segment 5 distinctly shorter than 4; dactyls short.

Pleon plate 3, hind corner acuminate. Urosome 2 nearly totally occluded dorsally by segment 1 & 3. Uropod 2, outer ramus 2/3 length of inner ramus. Uropod 3, inner ramus with 5 serially paired marginal spines. Telson linguiform, relatively narrow, length nearly twice width, apex sharply rounded.

Distribution. From southeastern Alaska to central California (Dillon Beach), mostly under boulders, associated with sessile invertebrates, *Egorgia*, *Corallina* and other algae, at LW level.

Etymology. From the Latin "*serratus*", with reference to the serrated hind margins of the gnathopod dactyls.

Taxonomic commentary. *Gnathopleustes serratus* is relatively primitive species in characters of the mouthparts (maxilliped) and gnathopods (serrated dactyls), and near the base of the genus phylogenetically.

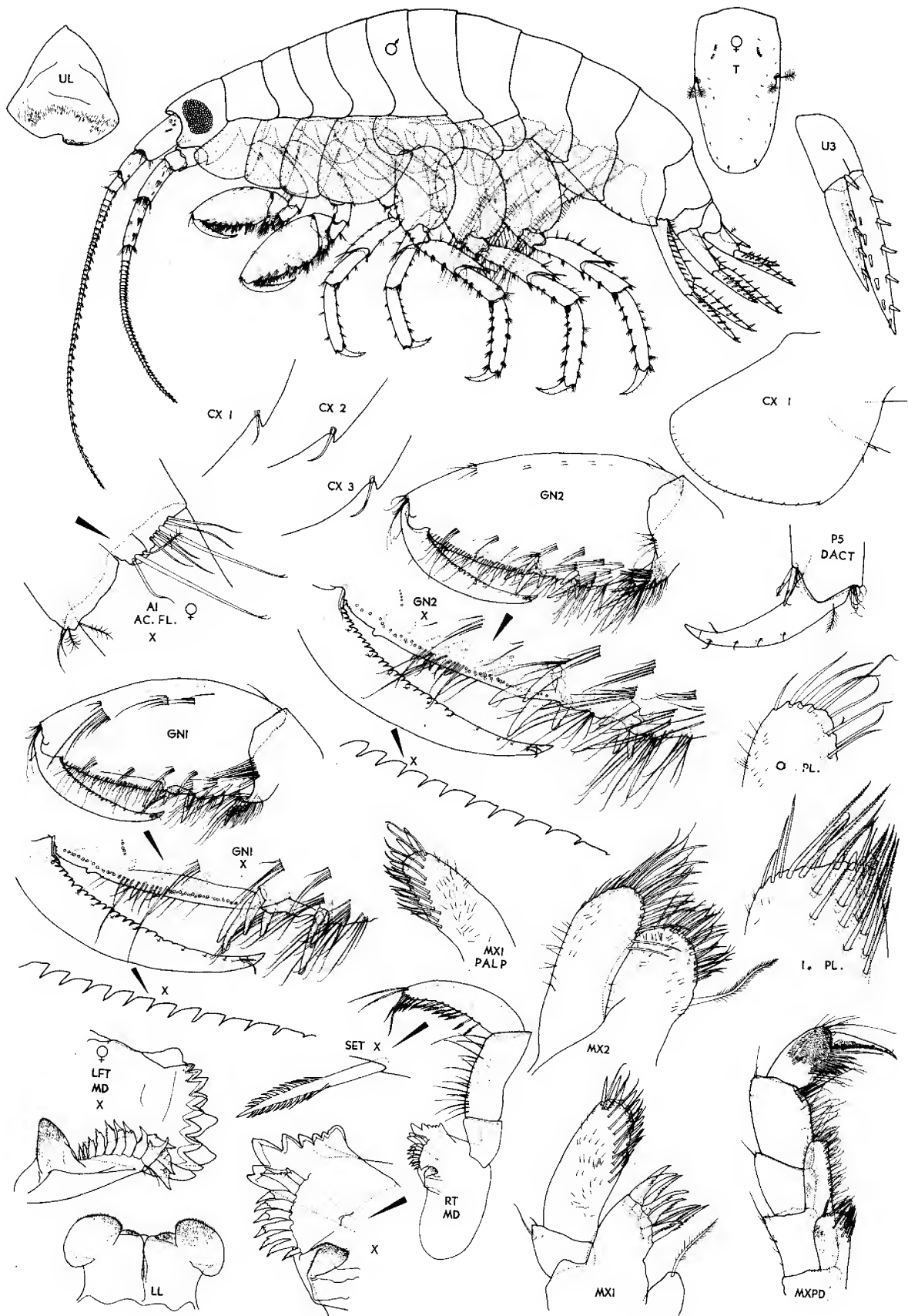


FIG. 21. *Gnathopleustes serratus*, new species. Male (8.5 mm); female (10.0 mm). Graham I., B. C.

Incisocalloipe J. L. Barnard

Incisocalloipe J. L. Barnard, 1959: 22.

Parapleustes Gurjanova, 1951: 645 (part.).—Barnard & Given, 1960: 42 (part.).—Gurjanova, 1972: 131 (part.).—Watling & Maurer, 1973: 1 (part.).—Barnard & Karaman, 1991: 649 (part.).—Ishimaru, 1994: 46 (part.).

Parapleustes (*derzhavini* group) Ishimaru, 1984: 407, 450.

Type species. *Incisocalloipe newportensis* Barnard, 1959, original designation.

Species composition. *Incisocalloipe dilatatus* (Ishimaru, 1984); *I. bairdi* (Boeck, 1871); *I. derzhavini* (Gurjanova, 1938); *I. nipponensis*, new species; *I. makiki* (J. L. Barnard, 1970); *I. aestuarius* (Watling & Maurer, 1973); *I. filiaris* (Hirayama, 1988).

Diagnosis. Body small to medium, slender, smooth above. Head, rostrum short, little exceeding rounded anterior head lobe. Eye small, medium rounded to ovate. Antennal flagella slender, nearly bare; antenna 1 longer than antenna 2. Antenna 1, peduncular segments 2 & 3 short, peduncle 1 lacking postero-distal cusp; accessory flagellum minute, triangular.

Mouthparts modified. Upper lip, median notch deep, lobes asymmetrical. Lower lip broad, squat, outer lobes steeply oblique. Mandible, molar reduced to a small setulose knob; left lacinia 9-12 dentate; blades numerous (9-14), unmodified; incisors 8-dentate; palp segment 2 medially sparsely setose, segment 3 longest, apically truncate, segment 1 medium. Maxilla 1, inner plate with 1 apical seta; outer plate with 9 medium strong pectinate spine-teeth; palp not broadened, surface setulose, apex rounded, with few spines, segment 1 with lateral seta(e). Maxilla 2, inner plate little broadened, inner margin with single large plumose seta. Maxilliped, inner plate with few (2-4) "button" spines; segment 3 longer than palp segment 2; outer plate columnar, palp segment 3 largest, segment 3 often with short inner distal spine-teeth; dactyl slender.

Coxal plates 1-4 medium deep; coxa 4 largest & strongly excavate behind; coxa 1 shortest, slightly expanding distally; hind cusps small, single or double. Gnathopods 1 & 2, variously (mainly strongly) subchelate, subequal, not sexually dimorphic. Gnathopod 1, basis normal, anterior margin often strongly setose; meral process weak; carpus short, deep; propod, palm convex, with median tooth, not continuous with weakly setose posterior margin; postero-distal angle with 2-3 spine groups not extending onto palm.

Peraeopods of medium length and stoutness, segments spinose but not setose; segment 4 slightly longer than and distally overhanging segment 5; dactyls medium, curved. Peraeopods 5-7 homopodous, increasing slightly posteriorly; coxae medium deep, rounded behind; bases broad, hind margin nearly flat.

Pleon segments normal, hind corners acuminate (but not

hooked), lower margins lightly spinose. Pleopods normal, not sexually dimorphic, rami medium strong. Uropods 1 & 2 extending to or beyond uropod 3, rami spinose. Uropod 1, inner ramus slightly the longer. Uropod 2, outer ramus distinctly the shorter. Uropod 3, rami relatively short, inner ramus distinctly the longer.

Telson medium long, keeled proximally below, apex rounded, with small paired notch and seta.

Coxal gills undescribed. Brood plates large, broad.

Taxonomic remarks. *Incisocalloipe* is phyletically the most advanced genus, with closest relationships to *Gnathopleustes* and, to some extent, to *Trachypleustes*. These groups may be distinguished by a combination of character trends, as outline in the key and Table I. (p. 128).

Distributional ecology. Species of *Incisocalloipe* occur mainly in temperate or subtropical regions of pan-Pacific and North Atlantic regions, in shallow occasionally estuarine habitats. By contrast, the slightly less phyletically advanced members of *Gnathopleustes* are confined to open coast habitats of the North American Pacific region, but some (e.g., *G. pachychaetus*) exhibit brackish-water tolerance.

Incisocalloipe newportensis Barnard

(Fig. 22)

Incisocalloipe newportensis Barnard, 1959: 22, pl. 2.

Parapleustes pugettensis Barnard & Given, 1960: 43, fig. 4.—Barnard, 1969b: 178.—Barnard & Karaman, 1991: 650.

Material examined. J. L. Barnard's type specimen (Stn. #9, AHF- # 522) has been made available for this study, courtesy of the Los Angeles County Museum.

Diagnosis. Female (5.0 mm): Head, eyes medium, oval, black. Antennae especially peduncles, stout. Antenna 1 the longer; peduncular segment 1 large, 2 & 3 short; flagellum long. Antenna 2, peduncular segment 5 > segment 4.

Mandible, spine row with 8-9 blades; left lacinia 8-9 dentate; palp segment 3 with 6-7 posterior marginal pectinate "D" spines. Maxilla 1, palp segment 2, surface setulose, segment 1 with single "shoulder" seta. Maxillas 2, inner plate broad, short. Maxilliped, inner plate with button spines.

Coxal plate 1 large, expanding distally, little shorter than 2, with single postero-distal cusp. Coxa broad, width = depth. Gnathopods strongly subchelate, propods medium large; basis, anterior margin with a few scattered short setae; hind margin with a few setae proximally. Gnathopod 2, basis, anterior margin nearly bare.

Peraeopods 3 & 4, segment 5 short, length < segment 5; Peraeopods 5-7, bases broad, convex behind; segment 5 short dactyls strong.

Pleon plate 3, hind corner acuminate, hind margin nearly straight. Uropod 1, peduncle, outer margin strongly spinose.

KEY TO SPECIES OF *INCISOCALLIOPE*

1. Coxa 1 distinctly shorter than coxa 2; gnathopod 1, basis, anterior margin strongly setose (20+ setae); peraeopods 3 & 4, basis, anterior margin lined with short setae throughout 2.
—Coxa 1 about as deep as coxa 2; gnathopod 1, basis, anterior margin nearly bare or with fewer than 15 setae; peraeopods 3 & 4 basis, anterior margin weakly setose 3.
2. Uropod 2, rami subequal; peraeopod 7, basis medium broad, postero-distal lobe ordinary, not reaching to segment 4; dactyls short, < 1/3 segment 6 *I. aestuarius* (p. 104)
—Uropod 2, outer ramus distinctly (1/3) the shorter; peraeopod 7, basis narrow, hind lobe deep, reaching segment 4 behind; dactyls heavy, strong, >1/3 segment 6 *I. filialis* (p. 102)
3. Gnathopods 1 & 2, propods relatively weak, depth not greater than carpus; gnathopod 1, basis with antero-distal cluster of 3 long setae 4.
—Gnathopods 1 & 2, propods relatively stout, strong, depth greater than carpus; gnathopod 1, basis antero-distally with 0-2, or 4, long setae 5.
4. Gnathopod 2, basis with 2 strong antero-distal setae; antenna 1, peduncular segment 1 large, distinctly longer than segments 2 & 3 combined *I. derzhavini* (p. 102)
—Gnathopod 2, basis lacking strong antero-distal setae; antenna 1, peduncle 1 ordinary, length about equal to segments 2 & 3 combined *I. nipponensis* (p. 100)
5. Gnathopod 1, basis, anterior marginal setae long, length > width of basis; antenna 2, peduncular segment 5 not longer than 4 *I. makiki* (p. 98)
Gnathopod 1, basis, anterior marginal setae short, length < width of basis; antenna 2, peduncular segment 5, length distinctly > segment 4 6.
6. Peraeopods 3 & 4, segment 5 regular, length ~ segment 4; antenna 2, peduncular segments 4 & 5 slender, length 3-4 X width *I. bairdi* (p. 96)
—Peraeopods 3 & 4, segment 5 short, thick, length < segment 4; antenna 2, peduncular segments 4 & 5 relatively short, thick, length ~2X width 7.
7. Peraeopod 4, coxa broad, width ~depth; uropod 1, peduncular outer margin lined with 10-12 strong spines; uropod 3, inner ramus with 5-6 pairs of marginal spines . . . *I. newportensis* (p. 95)
—Peraeopod 4, basis narrow, width < depth; uropod 1, peduncular margin proximally with cluster of 3-4 stout spines; uropod 3, inner ramus, margins with 3-4 pairs of spines. *I. dilatatus* (p. 97)

Uropod 2, outer ramus ~3/4 inner ramus. Uropod 3, inner ramus with 6 pairs of marginal spines. Telson long, apex truncated.

Taxonomic and distributional commentary. The type locality of *Incisocalliope newportensis* is Newport Bay, California. The species has been recorded authentically on the eastern Pacific coast only south of Pt. Conception. It has been confused with *Gnathopleustes pugettensis*. However, morphological differences are major, and the latter is also larger at maturity and more northerly in distribution.

Incisocalliope newportensis and *I. bairdi* (J.L. Barnard) form a primitive species pair within the genus. Further species of the genus may yet be discovered, especially in the Baja and Gulf of California regions, and in the southern Sea of Japan and China Sea regions. Differences noted here between this pair and the remaining six species may eventually form a basis for recognition of the two phyletic groups at the subgeneric level (Fig. 43, p. 127).

***Incisocalliope bairdi* (Boeck)**
(Fig. 23)

Paramphitoe bairdi Boeck, 1871: 45-46, 50, pl. 1, fig. 3.—Barnard, 1956: 36, Plate 12.—Barnard & Karaman, 1991: 650.

Neopleustes bairdi Stebbing, 1906: 314-315.

non Parapleustes pugettensis Barnard & Given, 1960.

Diagnosis. Male (5.5 mm): Head, eyes medium large, oval-round, black. Antenna 1 the longer, flagellum 36-segmented. Antenna 2, peduncular segment 4 & 5 slender, segment 5 > 4.

Mandible, spine row with 15 blades; lacinia with 9 teeth; palp segment 3 with 9-10 posterior marginal "D" spines. Maxilla 1, palp segment 2, apex with 7 spines and facial setal row, segment 1 with 2 short "shoulder" setae. Maxilla 2, plates small, inner plate not broadened. Maxilliped, inner plate with 4-5 apical marginal "button" spines outer plate columnar; palp segment 3 large, heavy.

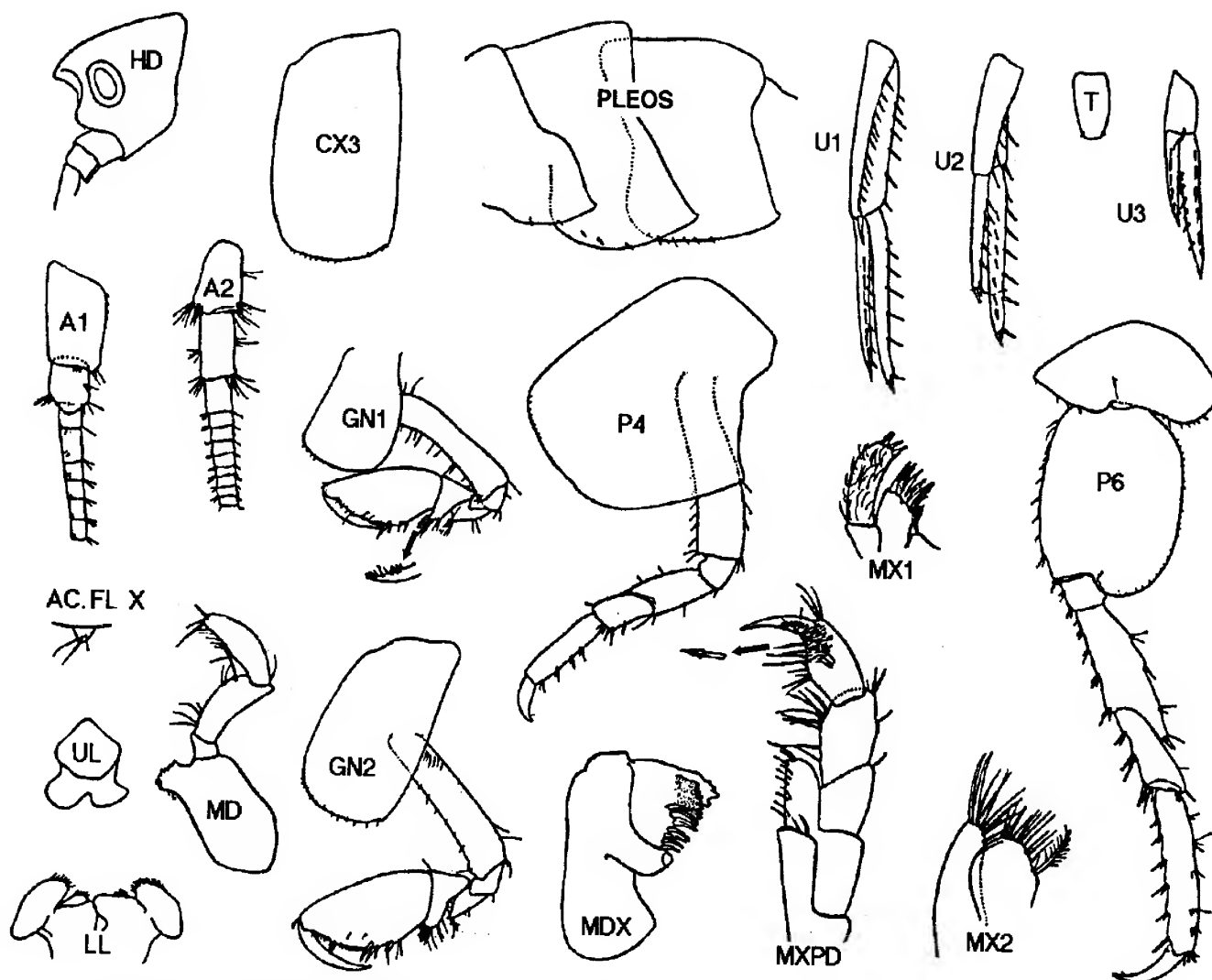


FIG. 22. *Incisocalloipe newportensis* (Barnard 1959). Female (5.0 mm). New port Bay, California.

Coxal 1 large, broadening distally, lower margin gently convex, with single postero-distal cusp. Coxa 4 narrow, width < depth. Gnathopods large, strongly subchelate. Gnathopod 1, basis, anterior and posterior margins nearly smooth; merus with short distal process; propod, hind margin straight, with single distal setal group. Gnathopod 2, hind margin of coxa with 2-3 short spines; basis nearly bare of setae.

Peraeopods 3 & 4, segment 5 not shortened, length ~ segment 4. Peraeopods 5-7, bases medium broad, hind margins nearly straight; segment 5 not shortened. Dactyls medium.

Pleon 3, hind corner acuminate, Uropod 1, peduncular outer margin with 7-8 spines, outer ramus very slightly the shorter. Uropod 2, outer ramus about 3/4 length of inner ramus. Uropod 3, inner ramus with 5 pairs of marginal spines. Telson medium, narrowing to smoothly rounded apex.

Taxonomic commentary. The species was first described by Boeck (1872) from southern California, and

rediscovered in fresh material from the same region by J. L. Barnard (1956). Barnard's description and figures, more detailed than the accounts of Boeck (loc. cit.) and Stebbing (1906) form the basis of the present analysis.

Incisocalloipe dilatatus (Ishimaru)
(Fig. 24)

Parapleustes dilatatus Ishimaru, 1984: 425, figs. 17-20.—
Barnard & Karaman, 1991: 650.—Ishimaru, 1994: 54.

Diagnosis. Male (4.7 mm): Head, eye medium large almond-shaped, black. Antennae relatively short, first slightly the longer. Antenna 1, peduncular segment 1 short, thick; flagellum 27-segmented. Antenna 2, peduncular segments 4 & 5 relatively long, slender, $5 > 4$; flagellum 18-segmented.

Mandible, spine row with 10 blades; left lacinia 9-dentate; palp segment 3 with 6 posterior marginal "D" spines. Maxilla 1, palp segment 1 with 2 "shoulder" setae; segment 2, apex oblique, with 4 spines and numerous facial

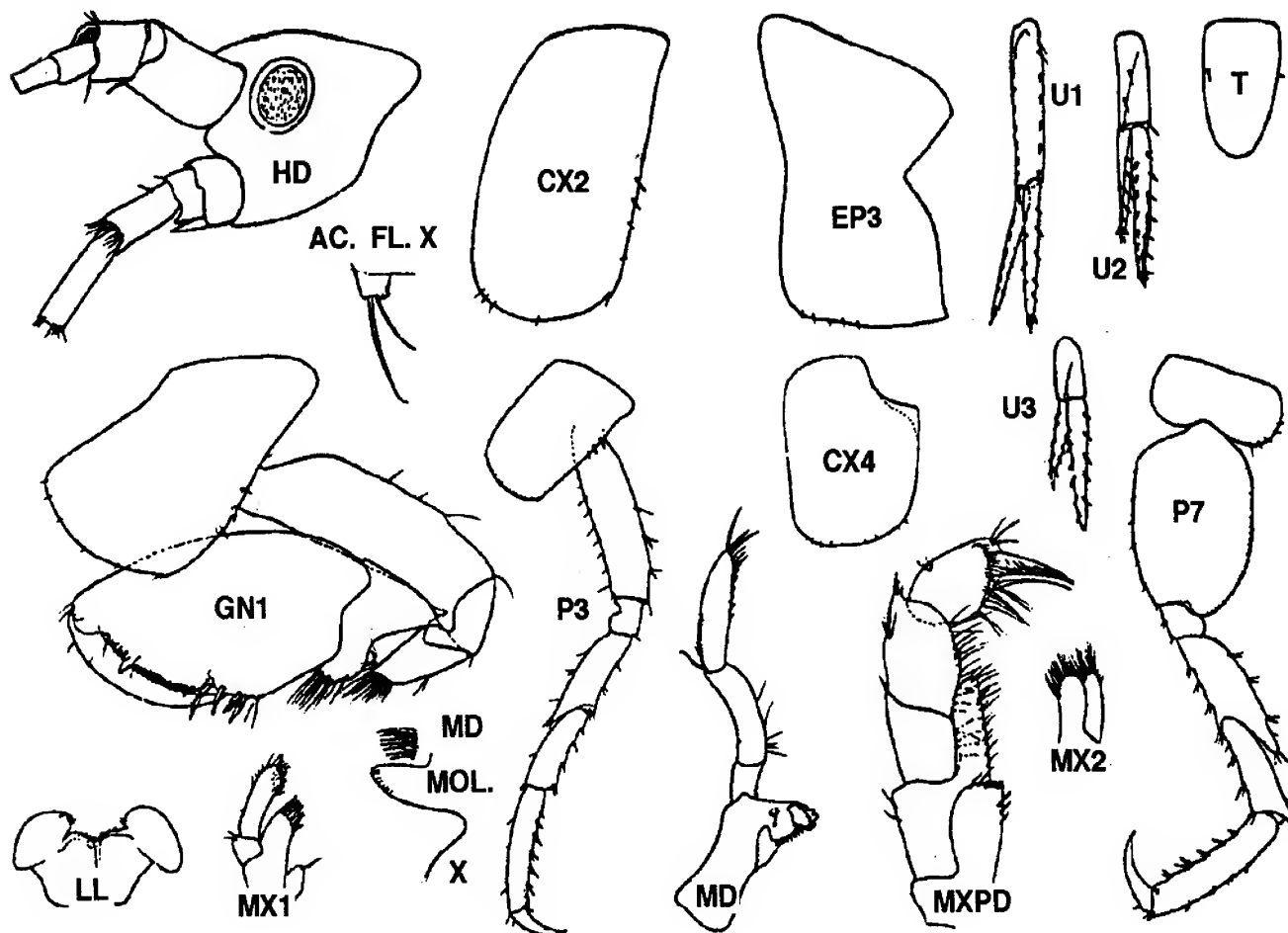


FIG. 23. *Incisocallope bairdi* (Boeck, 1971). Male (5.5 mm). S. California. (after Barnard, 1956).

setae. Maxilla 2, inner plate very slightly broadened. Maxilliped, inner plate with 3 apical "button" spines; outer plate, with 2 slender apical spines; palp segment 3 with distal inner facial scales.

Coxal plate 1 large, distal margin convex, hind corner with 2 small cusps, posterior margin with 2 short spines. Coxa 4 medium, depth > width. Gnathopods strongly subchelate, propods relatively large. Gnathopod 1, basis with 1-2 stout anterior marginal setae, hind margin nearly bare; merus lacking postero-distal process; propod with superior medial facial cluster of setae; hind margin with single distal setal group. Gnathopod 2, anterior and posterior margins with weak, short setae; merus with strong postero-distal process.

Peraeopod 3 & 4, segment 4 short, length > segment 5, dactyl medium. Peraeopods 5-7, bases broad, rounded behind; segment 5 short, length < segment 4.

Pleon plate 3, hind corner acuminate. Uropod 1, peduncular outer margin relatively weakly spinose, with cluster of 3 strongest spines proximally; rami weakly marginally spinose; outer ramus distinctly the shorter. Uropod 2, peduncle with 2 strong outer marginal spines. Uropod 3, rami short, inner ramus with 3-4 marginal spines. Telson

relatively short narrowly slightly to broadly rounded apex. Female (6.0 mm). No discernible difference from the male

Taxonomic commentary. *Incisocallope dilatatus* is morphologically closest to *I. makiki* Barnard from the Hawaiian Islands (Fig. 44, p. 129). Both are members of the advanced subgroup that includes, *I. derzhavini* and *I. filialis* of the western Pacific region.

Distribution. Japan Sea, southern shores of Hokkaido, under marine algae, LW level. Females ov., May to August.

Incisocallope makiki (J. L. Barnard)
(Fig. 25)

Parapleustes derzhavini makiki Barnard, 1970: 227.

Diagnosis. Female (4.2 mm): Head, eye medium large, reddish or dark brownish, irregularly roundish. Antenna 1, peduncular segment 1 large > 2 & 3 combined, flagellum 24+ segmented. Antenna 2, peduncular segment 4 & 5 medium stout, subequal, flagellum 18+ segmented.

Mandible, spine row with 8 blades, left lacinia 10-11-

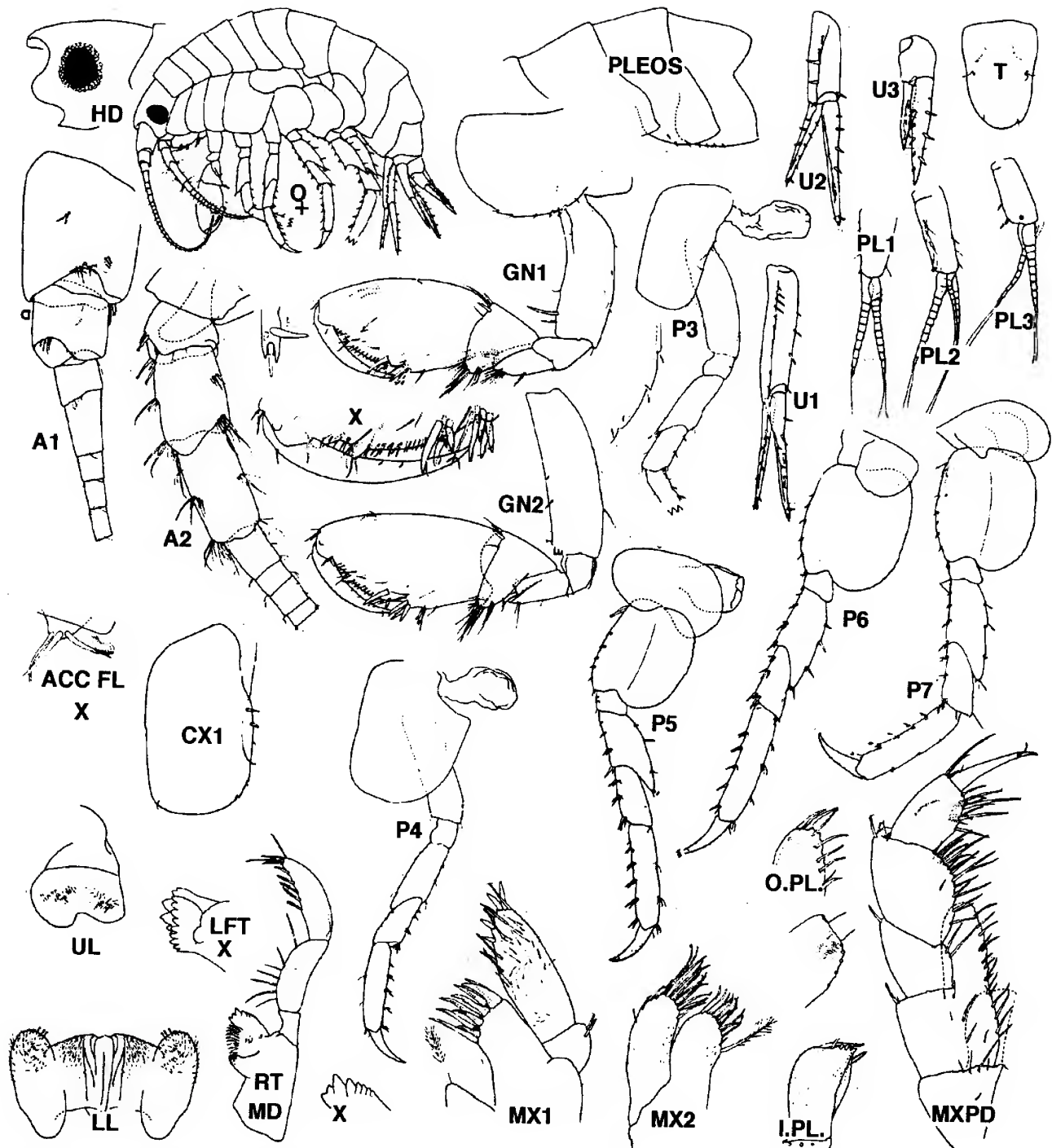


FIG. 24. *Incisocalloiope dilatatus* (Ishimaru, 1984). Male (4.7 mm). Hokkaido. (after Ishimaru, 1984).

dentate; palp segment 3, inner margin with 7 pectinate "D" setae. Maxilla 1, inner plate small, with 1 apical seta. Maxilliped, inner plate with 2 apical "button spines; outer plate with 2 slender apical spines; palp segment 3, with pectinations or scales at base of dactyl.

Coxa 1 medium large, lower margin convex, hind corner with 1-2 cusps, hind margin with single spine. Coxa 2 with 1 postero-distal cusp. Coxa 4 broad, as wide as deep. Gnathopods strongly subchelate; propod of gnathopod 2 larger than 1. Gnathopod 1, basis, anterior margin with

numerous (~10) strong setae, each longer than width of basis, hind margin weakly setose proximally?; merus lacking distal process 1; propod with superior facial group of 2 setae; posterior margin bare. Gnathopod 2, basis virtually lacking marginal setae; merus with postero-distal process; propods, hind margin with distal group of spines and setae.

Peraeopods 3 & 4, basis, margins weakly short-setose; segment 5 slightly shorter than 4; segment 6, hind margin spinose. Peraeopods 5-7, basis moderately broad, hind margins convex, lower hind lobe shallow, not reaching

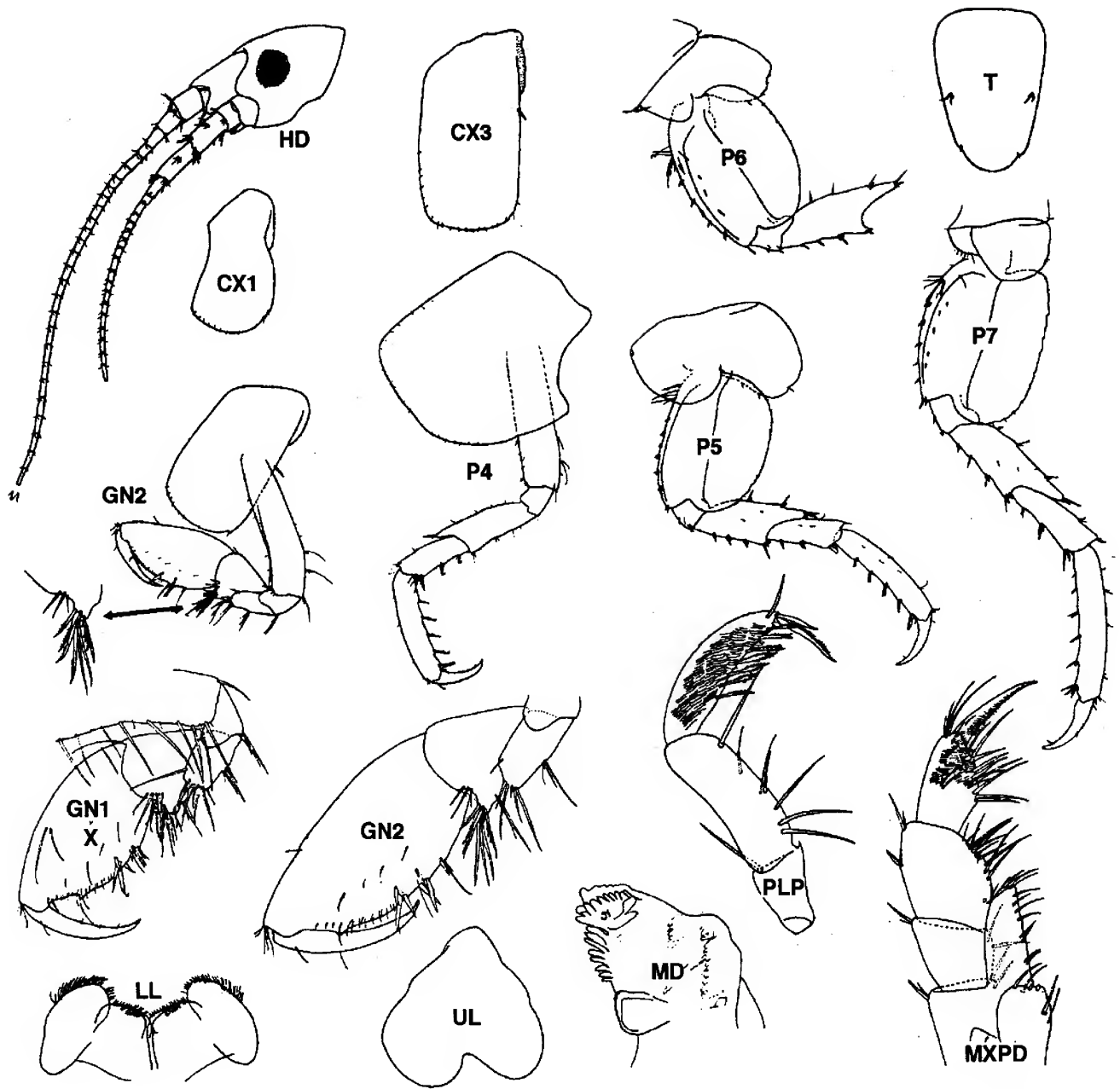


FIG. 25. *Incisocalloipe makiki* (J. L. Barnard). Female (4.2 mm). Hawaii (after Barnard, 1970).

segment 4; segment 5 shorter than segment 4.

Pleon 3, hind corner minutely acuminate. Uropods 1 & 2 strong. Uropod 1, peduncle, outer margin strongly spinose; outer ramus distinctly the shorter. Uropod 3, inner ramus slender, margins with 6 spines. Telson short, broad, little longer than wide, normally rounding apically.

Distribution. Oahu, Hawaiian Islands; 3-4 m in depth.

Taxonomic commentary. *Incisocalloipe makiki* merits full species status here. Its presumed common ancestor with *I. dilatatus* may have penetrated the Hawaiian archipelgo in the early Tertiary Period (p. 130).

Incisocalloipe nipponensis, new species
(Fig. 26)

Parapleustes derzhavini Ishimaru, 1984: 417.--Ishimaru, 1994: 54 (part.)

Diagnosis. Female (5.0 mm): Head, eye small, rounded, black. Antenna 1, peduncular segments 1-3 short, segment 1 = 2 and 3 combined; flagellum, slender 25-segmented. Antenna 2, peduncular segment 4 shorter than 5, medium thick; flagellum slender, 24-segmented.

Mandible, spine row with 8 blades; left lacinia 11-dentate; palp segment 3 with 7 posterior marginal "D" setae.

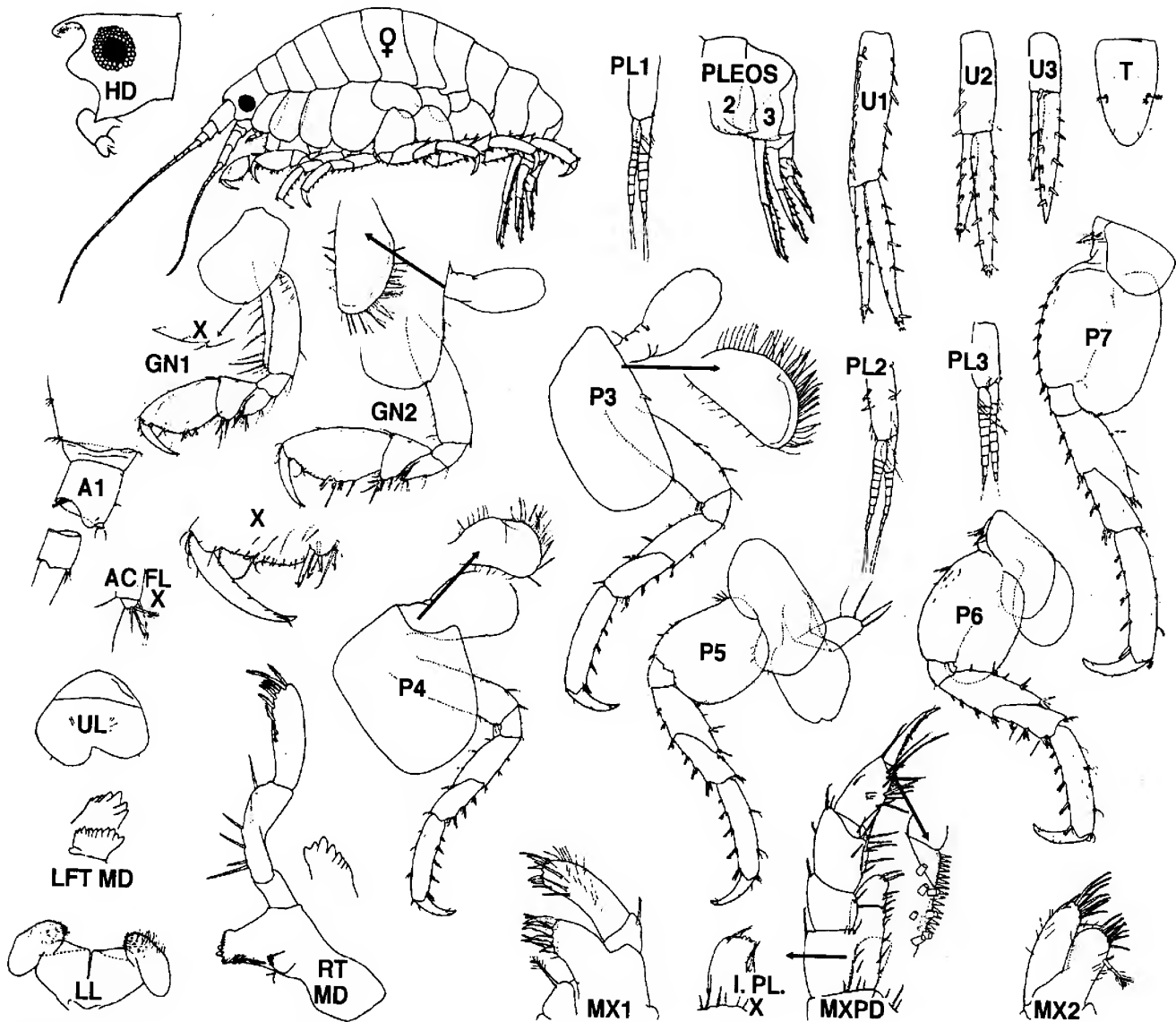


FIG. 26. *Incisocalloiope nipponensis*, new species. Female (4.6 mm). Japan Sea. (after Ishimaru, 1984).

Maxilla 1, palp segment 1 with single "shoulder" seta; segment 2 apically with 4 spines and facial row of 3 setae. Maxilla 2, inner plate short, not broadened. Maxilliped, inner plate with 3 "button" spines; outer plate with 2 apical slender spines; palp segment 3 with distal inner marginal pectinations.

Coxa 1 small, 1/3 shorter than 2, with single postero-distal cusp and 1-2 posterior marginal short spines. Coxa 4 medium broad, not as wide as deep. Gnathopods relatively weakly subchelate, propods only slightly broadened. Gnathopod 1, basis with 15+ long anterior marginal setae and ~10 short postero proximal marginal setae, merus with distal cusp; propod, hind margin with single distal spine. Gnathopod 2, basis, margins nearly bare merus with acute postero-distal cusp.

Peraeopods 3 & 4, regular, segment 5 not noticeably shortened, dactyls medium. Peraeopods 5-7, base broadly expanded, hind margins convex, dactyls stout.

Pleon plate 3, hind corner strongly acuminate. Uropod 1, peduncle, outer margin strongly spinose. Uropod 2, inner ramus longer than peduncles, 1/3 longer than outer ramus. Uropod 3, inner ramus 1/3 longer than outer ramus, with 4-5 pairs of marginal spines. Telson medium long, narrowing to sharply rounded apex.

Type material. Female "a" (5.0 mm) **Holotype**; Stn. 4, Samani, au 5 1982. Hokkaido, (Sea of Japan coast); also 2 females. **Paratypes**, at stations 2-4 along south coast of Hokkaido, 0.5 m depth, among algae. Collections of the Zoological Museum, Faculty of Science, Hokkaido University.

Distribution. Shores of Hokkaido, LW to 5 m depth Sargassum belt, Laminaria belt; among *Leathesia* and other algae scraped from surface of boulders.

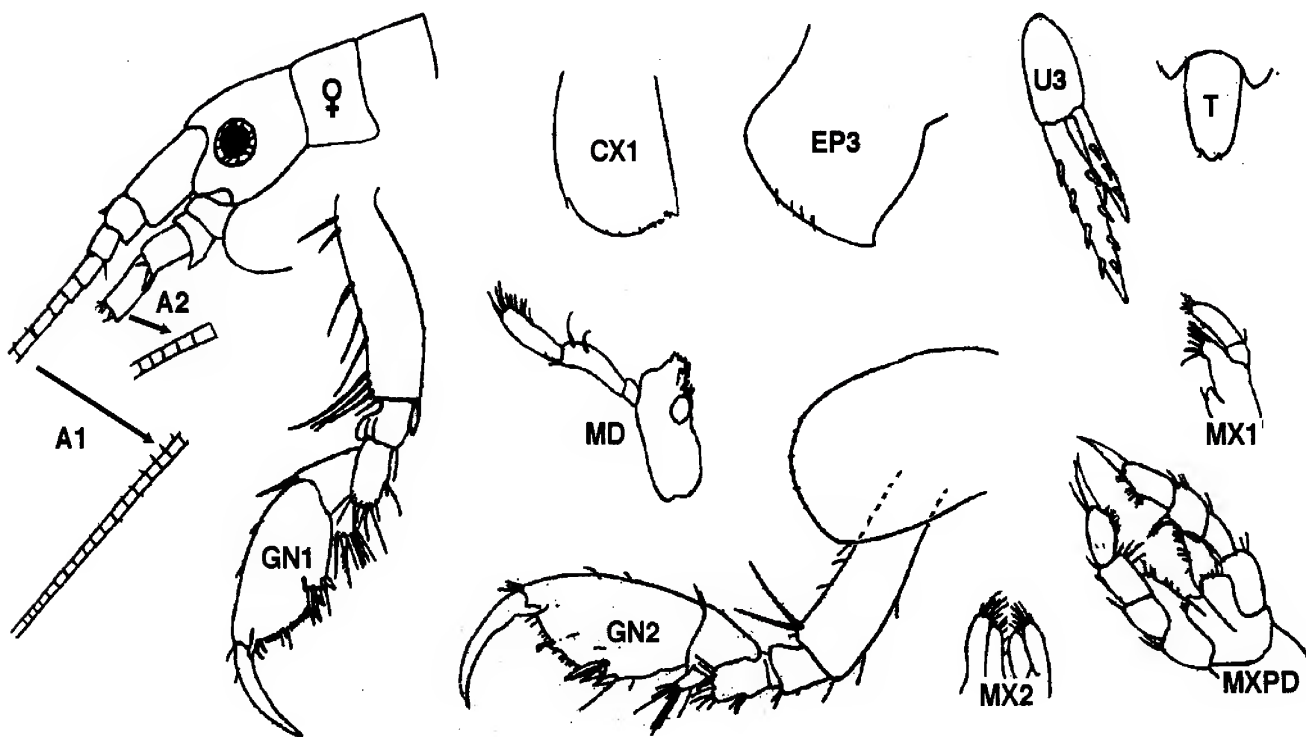


FIG. 27. *Incisocalloipe derzhavini* (Gurj., 1938). Female (4.0 mm). Japan Sea. (after Gurjanova, 1951).

Taxonomic commentary. This description is based on the careful work of Ishimaru (1984). He had previously found it very similar to the female (4.0 mm) of *Neopleustes derzhavini* from the sea of Japan, described by Gurjanova (1951), that is treated below (see also Fig. 27).

Incisocalloipe derzhavini Gurjanova
(Fig. 27)

Neopleustes derzhavini Gurjanova, 1938: 317, fig. 31.
Gurjanova, 1951: 645, fig. 442.

Parapleustes derzhavini Barnard & Karaman, 1991: 650 (part)

Diagnosis. Female (4.0 mm): Head, eyes medium, round, black. Antenna 1, peduncle 1 large, length > segments 2 & 3 combined; flagellum medium long, slender, 25-27 segmented. Antenna 2, peduncular segment 4 & 5 short, thick, 5 > 4; flagellum 18-segmented.

Mandible, spine row with 6-8 blades; palp segment 3 with 5-6 pectinate "D" spines. Maxilla 1, palp segment 1 with 1 shoulder seta; segment 2, rounded apex with 4 spines. Maxilla 2, inner plate not broadened. Maxilliped, inner plate with 3 (?) button spines, palp segment 3 with pectinations at base of dactyl?

Coxa 1 relatively short, little broadening distally, lower margin convex, with 1 hind cusp. Gnathopods relatively

weakly subchelate; propods not deeper than respective carpus. Gnathopod 1, basis, anterior margin with 9-10 stout setae, concentrated distally, mostly longer than width of basis; merus lacking distal process; propod hind margin bare. Gnathopod 2, basis, antero-distal margin with 2 very large stout setae, hind margin nearly bare; merus with short distal process?, propod, hind margin with single distal seta.

Peraeopods 3 & 4 ordinary. Peraeopods 5-7 ordinary; bases moderately expanded, ovate.

Pleon plate 3, hind corner acuminate, lower margin gently convex, with 4-5 small spines. Uropod 3, inner ramus slender, margins each with 4 spines. Telson medium long, narrow, sharply rounding at apex.

Distributional ecology. Japan Sea; tidal zone.

Taxonomic commentary. Gurjanova's original figures and description are limited but sufficiently detailed to separate *I. derzhavini* from the material of Ishimaru (loc. cit.) described above as *I. nipponensis*, new species.

Incisocalloipe filialis (Hirayama)
(Fig. 28)

Parapleustes filialis Hirayama, 1988: 40, figs. 265-268.—Barnard & Karaman, 1991: 650.—Ishimaru, 1994: 54.

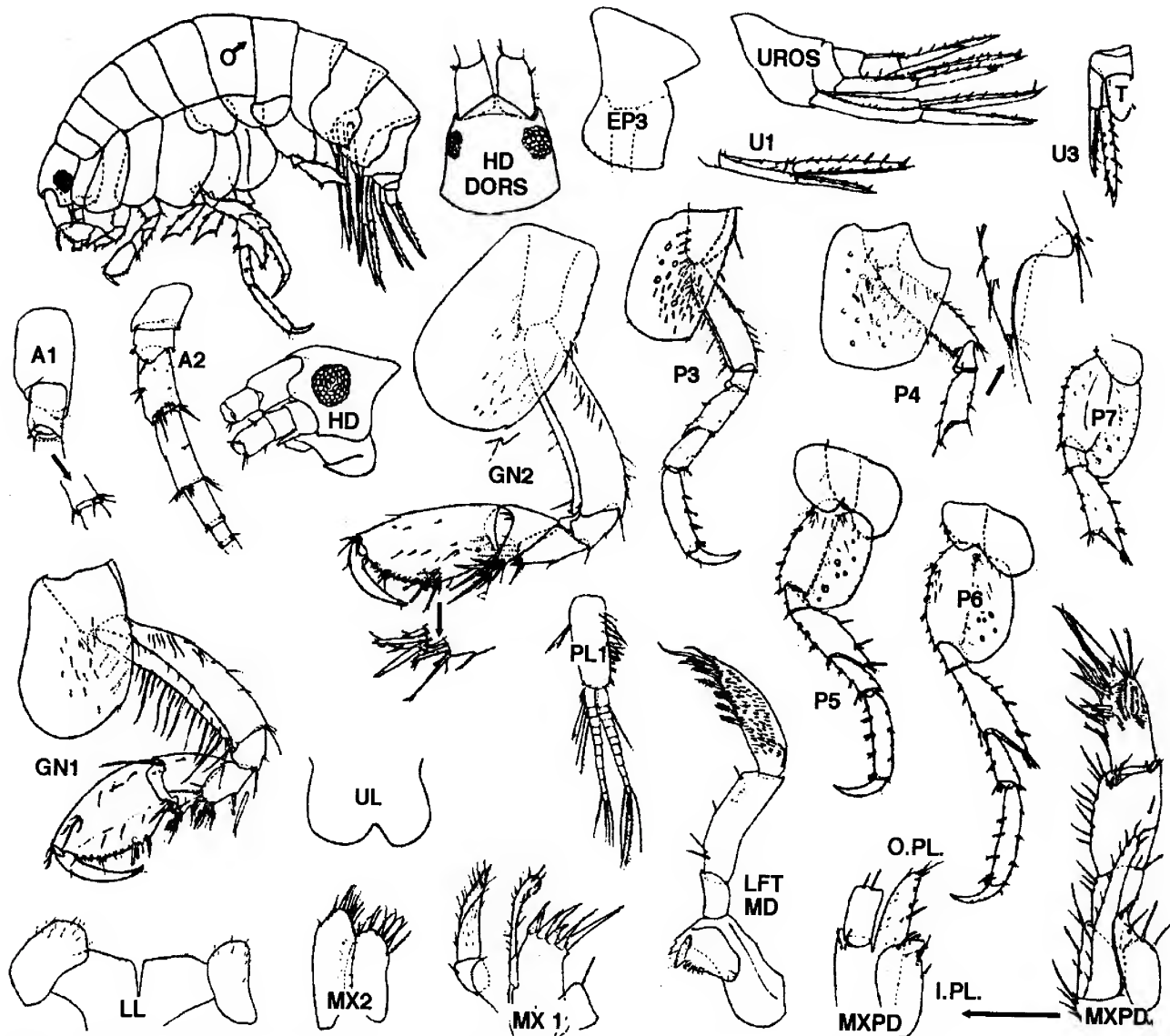


FIG. 28. *Incisocallope filialiss* (Hirayama). Male (3.5 mm). Ariake Sea, Japan. (after Hirayama, 1988).

Diagnosis. Male (3.5 mm): Body small, pleonites slightly raised postero-dorsally. Head, eyes medium large, nearly round, black. Antennae slender, medium long. Antenna 1, peduncular segment 2 short, ~1/2 segment 1; flagellum ~15-segmented. Antenna 2, peduncular segments 4 & 5 stout, 5 slightly the longer; flagellum 16-segmented.

Upper lip with relatively deep V-notch, lobes asymmetrical. Lower lip inner lobes broad, outer lobes oblique. Mandible, molar process small, vestigial; spine row with 6 short blades; incisor (left) with 4 proximal large teeth and 4-5 distal denticles; palp segment 3, basal "A" seta small, inner margin with 5-6 pectinate "D" spines; left lacinia 10-dentate. Maxilla 1, inner plate with single apical seta; palp segment 1 with single "shoulder" seta; distal segment, apex with 4-5 slender spines. Maxilla 2, inner plate short, not broadened, inner margin with single proximal plumose seta. Maxilliped, inner plate medium, inner margin notched distally, apex with 5 slender spines; outer plate slender, truncate apex with 2 slender spines; palp stout, segment 3 with distal

pectinate denticles at base of dactyl; dactyl slender, straight, length about equal to segment 3.

Coxal plates 1-3 lower margins broadly rounded, hind margins with 1-2 median short spines, hind corners each with single cusp. Coxa 1 distinctly shorter than 2. Gnathopod 1, anterior margin of basis strongly setose, (20+ setae), some setae longer than width of basis; hind margin of basis proximally with 6-8 shorter setae; carpus short, as deep as long, hind lobe stout; propod short, expanding distally, inner face with scattered setae; palmar margin convex, oblique slightly longer than hind margin, postero-distal angle with spine groups on either side of short dactyl-tip depression, distal spines larger; dactyl slender, with small distal unguis. Gnathopod 2, anterior margin of basis weakly setose, with single distal seta; hind margin proximally with row of setae; carpus short, hind lobe narrow propod subovate, longer and more slender than in gnathopod 1; two groups of longer and stronger spines at palmar angle.

Peraeopods 3 & 4 relatively short and stout; bases,

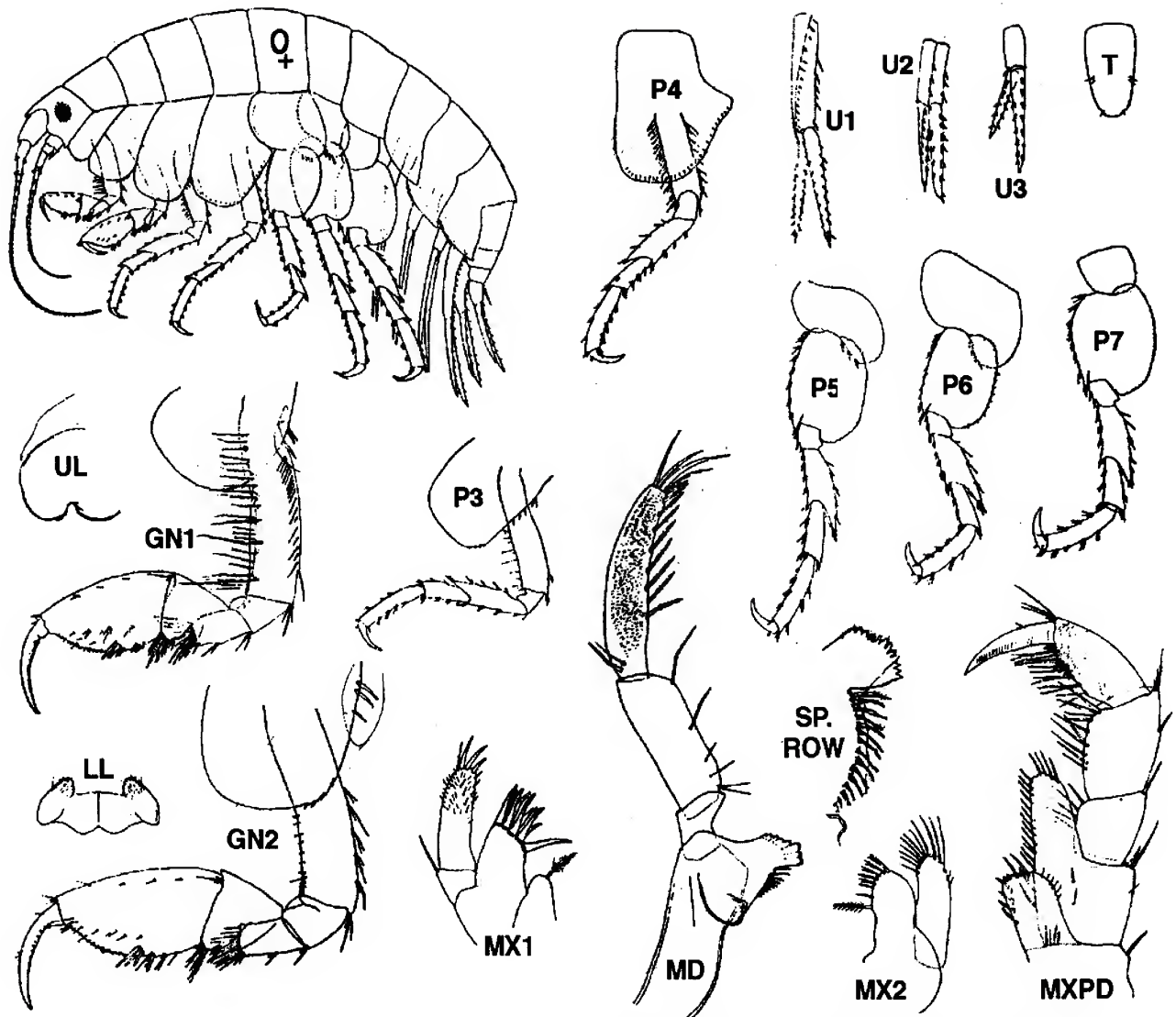


FIG. 29. *Incisocalloiope aestuarius* (Watling & Maurer, 1973). Female (4.0 mm). Delaware Bay.

anterior and posterior margins moderately strongly setose; segment 5 shorter than 4; segment 6, hind margin with 3 groups of stout spines; dactyl heavy, medium. Peraeopods 5-7, bases only moderately broadened, least in peraeopod 7, postero-distal lobes large, deep, reaching segment 4; segment 5 shorter than 4; dactyls stout.

Pleon plate 3, lower margin weakly spinose, hind corner squared, not acuminate. Pleopod peduncles, outer margin strongly setose. Uropods 1 & 2 large, extending well beyond uropod 3. Uropod 1, peduncle large, outer margin finely spinose. Uropod 2, outer ramus distinctly the shorter. Uropod 3, outer ramus long, length $\sim 2/3$ long inner ramus, with 6 pairs marginal spines. Telson oblong, apex subacute.

Distribution. Ariake Sea, Japan; sublittoral.

Taxonomic commentary. Hirayama likened *Incisocalloiope filialis* to *Incisocalloiope derzhavini* but found several species differences. The species is an atypical *Parapleustes*, with several features more reminiscent of *Gnatho-*

pleustes. These include the unlike gnathopod propods, narrow peraeopod bases; and in mouthparts, the broad lower lips, "shoulder" seta on palp of maxilla 1, etc. The species is close to *I. dilatatus* in the armature of the maxilliped palp.

Incisocalloiope aestuarius (Watling & Maurer)
(Fig. 29)

Parapleustes aestuarius Watling & Maurer, 1973: 252, figs. 1-4.—Fox & Bynum, 1975: 230.—Ishimaru, 1984: 431.—Barnard & Karaman, 1991: 650.

Diagnosis. Female (4.0 mm): Head, eye small round, black. Antenna 1, peduncular segment 1 large, stout, length about equal to segments 2 & 3 combined. Flagellum long, ~ 40 segments. Antenna 2, peduncular segments 4 & 5 short, medium, segment 5 > 4 ; flagellum ! 25-segmented.

Mandible, spine row with ~ 14 slender blades, distally largest; left lacinia 10-dentate; palp segment 3 with 8-9 slender pectinate "D" spines. Maxilla 1, segment 1 with

single shoulder seta; segment 2, with numerous short facial setae, rounded apex with 4 spines; outer plate, inner apical spine elongate. Maxilla 2, inner plate not broadened. Maxilliped, inner plate with 2-3 apical marginal "button" spines; outer plate with 4 apical slender spines; palp segment 3 distally with pectinations at base of dactyl.

Coxal plate 1 short, lower margin convex, hind corner with 2-3 cusps posterior margin with 2-3 stout spines. Coxa 4 little broadened deeper than wide. Coxa 5 deep. Gnathopods relatively weakly subchelate; basis, anterior margin lined with numerous (20+) setae some longer the width of basis, hind margin strongly lined with shorter setae; merus lacking distal cusp; propod relatively short, not deeper than carpus; with superior and inferior facial clusters of small setae; hind margin shorter than palm, with single distal setal group. Gnathopod 2, basis distal with short setae, hind margin distally with several setal groups; merus with short posterior tooth; propod, hind margin with 2 distal setal groups.

Peraeopods 3 & 4 basis, anterior margin strongly short-setose; segment 5 shorter than 4; dactyls relatively short. Peraeopods 5-7, bases moderately broadened, hind margins convex; segment 5 slightly shorter than 4.

Pleon plate 3, hind corner acuminate, slightly produced. Uropods 1 & 2 strong, rami longer than peduncle. Uropod 1, peduncle, outer margin strongly spinose; rami subequal. Uropod 2 outer ramus little shorter than inner, margins strongly spinose. Uropod 3 rami long, slender, inner ramus with 7 pairs of marginal spines. Telson medium long, apex rounded.

Distributional ecology: From Delaware Bay, Chesapeake Bay to Albemarle Sound and estuaries of the southeastern states, on wharf pilings, among bryozoans, hydroids, and other sessile invertebrates.

Taxonomic & distributional commentary. The original description (as *Parapleustes aestuarius*) is limited in a number of features, some of which were pointed out by Fox & Bynum (loc. cit.). The species is remarkably close morphologically to *Incisocalliope filialis* from the Sea of Japan. The relationship appears closely phyletic, but the disjunct distribution of the two forms defies explanation that is entirely satisfactory (see p. 130).

Trachypleustes, new genus

Type species. *Trachypleustes vancouverensis*, new species.

Species composition. *Trachypleustes trevori*, new species (and varieties: Pribilof Islands, San Juan Batista I).

Diagnosis. A group of small, smooth-bodied pleustids having short antenna 1 peduncular segments, unequal gnathopods, slender legs, slender unequal rami of uropods, and heavily chitinated, "molarized", or otherwise strongly modified mandibular blades.

Body smooth above, slender. Head small; rostrum slightly produced beyond subacute head lobe. Eyes large. Antennae slender, elongate. Antenna 1, peduncle 1 large, without postero-distal process; segment 2 medium short; accessory flagellum minute, triangular, with a few apical setae. Antenna 2, peduncular segments 4 & 5 subequal, setose; flagellum elongate.

Mouthparts strongly modified. Upper lip moderately incised and asymmetrical. Lower lip broad, squat, outer lobes oblique. Mandible, molar minute; spine row with few (4-6), strongly thickened and/or flattened blades; left lacinia irregularly 10-11 dentate; incisor multidentate; palp, segment 3 longest, medial pectinate setae numerous (12+); segment 2 sparsely setose medially. Maxilla 1, outer plate short, spines tall; palp long, apex with slender spines and setae, segment 1 lacking lateral setae; inner plate 1-setose. Maxilla 2, inner plate medium broad, with 1 large inner plumose seta; maxilliped, palp and dactyl strong; inner plate short, apex sloping, with 3-5 button-teeth and 4-6 inner marginal setae; outer plate narrow, apex and inner margin slender-spinose.

Coxal plates 1-4 increasing in size posteriorly; coxa 1 small, not expanded distally; coxa 2-4 deeper than body plates; lower margins nearly straight, with hind cusp. Gnathopods 1 & 2 weakly subchelate, similar in form but unequal in size, not sexually dimorphic; gnathopod 2 distinctly the larger. Gnathopod 1, basis weakly setose anteriorly; carpus shallow, more than half length of propod; length of palm oblique, with small median tooth; length about equal to smooth hind margin; postero-distal angle with 2 groups of spines; dactyl slender. Gnathopod 2, carpus shorter, hind lobe deeper, anterior margin about half length of propod; 2-3 spine groups at posterior angle.

Peraeopods 3-7 slender, dactyls normally developed. Peraeopods 5-7 normally homopodous; bases regularly broad and rounded behind; segment 4 (merus) postero-distal process strongly overhanging segment 5.

Pleon plates 1-3 regular; lower margins spinose, hind corners variously acuminate. Pleopods strong, not sexually dimorphic.

Urosome 2 not occluded dorsally. Uropods 1 & 2 slender, marginally strongly spinose; rami unequal, inner ramus longer than peduncle. Uropod 3, rami markedly unequal, strongly spinose. Telson medium, apex rounded; penicillate setae slightly proximal to mid point.

Coxal gills small to medium, saclike, largest on peraeopods 4 & 5.

Distributional commentary. Members of the genus are known only from northern parts of the North American Pacific coastal marine region, in association with sponges and large sessile invertebrates.

Etymology. A combining form of the Greek root "trachytés" roughness, and the generic name *Pleustes*, that alludes to the rough, molarlike appearance of the mandibular blades.

Taxonomic Commentary. This generic group is distinguished by the heavily molarized and pavementlike mandibular blades, the unequal, non sexually dimorphic gnathopods, slender pereopods, and the elongate, spinose uropod rami. Phyletically the genus *Trachypleustes* appears closest to *Gnathopleustes*, but more distant from *Incisocallope*.

***Trachypleustes vancouverensis*, new species**
(Fig. 30)

Material examined.
eBRITISH COLUMBIA.

Northern Vancouver I.: ELB Stn O1, Cape Scott, Experiment Bight, under boulders, among algae, LW level, July 18, 1959. - female ov. (4.5 mm), **Holotype** (slide mount), CMN Cat. no. NMCC1995-0086.

Diagnosis. Female ov. (4.5 mm): Head, rostrum prolonged beyond lateral head lobe; eye subquadrate. Antenna 1, peduncular segment 1 long, extending to midpoint of peduncular segment 4 of antenna 2; flagellum ~28-segmented. Antenna 2, length about equal to antenna 1; flagellum ~28-segmented.

Lower lip, inner lobes very broad, shallow. Mandible, molar process prominent, apex blunt; spine row distally with 4 thick short blades having rough, conical apices, and proximally with several short vestigial blades; cutting edge of incisor with 7-8 unequal teeth; palp segment 3 apex blunt, inner distal margin with 12 slender pectinate "D" spines; left lacinia large, broad, cutting edge with 10 small uneven teeth. Maxilla 1, palp slightly narrowing distally, rounded apex with 6 slender spines. Maxilla 2 outer plate narrow. Maxilliped, inner plate short, with 3 inner marginal plumose setae, and 4 apical button spines; outer plate slender, narrowly subtruncate, with 2 very slender spines; palp ordinary.

Coxae relatively deep, broad, hind corners with single small cusp. Gnathopod 1, propod about half size of propod of gnathopod 2; palmar margin smoothly continuous with posterior margin; proximal spine group at postero-distal angle with single spine and split-tipped seta; posterior margin distally with single spine and setae. Gnathopod 2, carpal lobe, some distal setae pectinate; propod stout, subovate; proximal spine group at postero-distal angle with 5 spines and split-tipped seta; posterior margin distally with small cluster of split-tipped setae.

Pereopods 3 & 4 ordinary, slender; segment 4, anterior margin with 3-5 tufts of slender spines; dactyls strong. Pereopods 5-7 closely homopodous; bases broad, hind margins smoothly convex; margins of segments 4-6 with cluster of short spines; segment 5 slightly shorter than 4; dactyls strong, curved.

Pleon plates 1-3, hind corners acuminate. Urosome 2 with free dorsal margin. Uropod 3, outer ramus relatively long, ~60% of inner ramus.

Telson distally with several dorsal setules; apex unevenly rounded. Coxal gills on pereopods 4-6 relatively large, broadly saclike.

Etymology. The name alludes to the type locality on Vancouver Island, British Columbia.

Distributional ecology. The species has been confirmed only for the type locality, Northern Vancouver Island, from under rock and algal habitats at LW level

Taxonomic commentary. The species name *vancouverensis* alludes to its known distribution on Vancouver Island, British Columbia.

***Trachypleustes trevori*, new species**
(Figs. 31, 32, 33)

Material examined. About 130 specimens taken at 23 localities, as follows:

ALASKA.

Pribilof Islands: D. B. Quayle coll., Nov. 23, 1965 - 1 female ov (slide mount).

Southeastern Alaska. ELB Stns., 1961: A168, Klokachef I - 1 female; A175, San Juan Batista I., under rock, among algae, LW level, July 26, 1961 - 1 female ov. (slide mount). BRITISH COLUMBIA.

Queen Charlotte Islands: ELB Stn. E14a, Onward Pt. Moresby I. July 13, 1957 - 1 ov. female (slide mount), 2 other specimens.

Northcentral coast. ELB Stns., July, 1964: H7, McCauley I. - 1 female ov; H65, Christie Pass - 2 females ov (slide mounts), 1 im. ELB, 1959, Stn. N22, off Banks I. - 1 male (slide mount), 1 female, 28 other specimens.

Northern Vancouver I.: ELB Stns., July, 1959: V5, Lemon Pt., Nigei I. - 1 female ov (Slide mount); O3, Grant Bay - 5 females ov (2 slide mounts).

Southern Vancouver I.: ELB Stns., July 1970: P702, Long Beach, south end, from algae and sessile invertebrates, under boulders, at LW level July 6 - 1 female; P719, Botanical Beach, from kelp and sponges, under boulders at LW level, Aug. 1 - 1 female ov.

ELB Stns., 1975: P2, Bamfield Marine Laboratory, from floating log fouling community at surface, July 23 - 1 male, 1 female, 2 im.; P5c, Taylor I., Trevor channel, from ascidians and sponges, under large boulder, July 25 - 2 males, 2 females.

ELB Stns., 1976: B4, Off Brady's Beach, naturalist's dredge, 60-70 m, sand & algae June 25 - 1 female; B7, Wouwer I., Broken I., from algae and sponges on bedrock walls at LW, June 27 - 1 male, 1 female; B11b, Wickininnish Bay, south end, LW sandy mud, June 29 - 2 females; B28, Edward King I., among algae, under boulders, LW, July 10 - 1 female.

ELB Stns., 1977: B13, Trevor Channel, off Brady's Beach, 6-14 m naturalist's dredge, sand, stone, algae, May 25, 1977

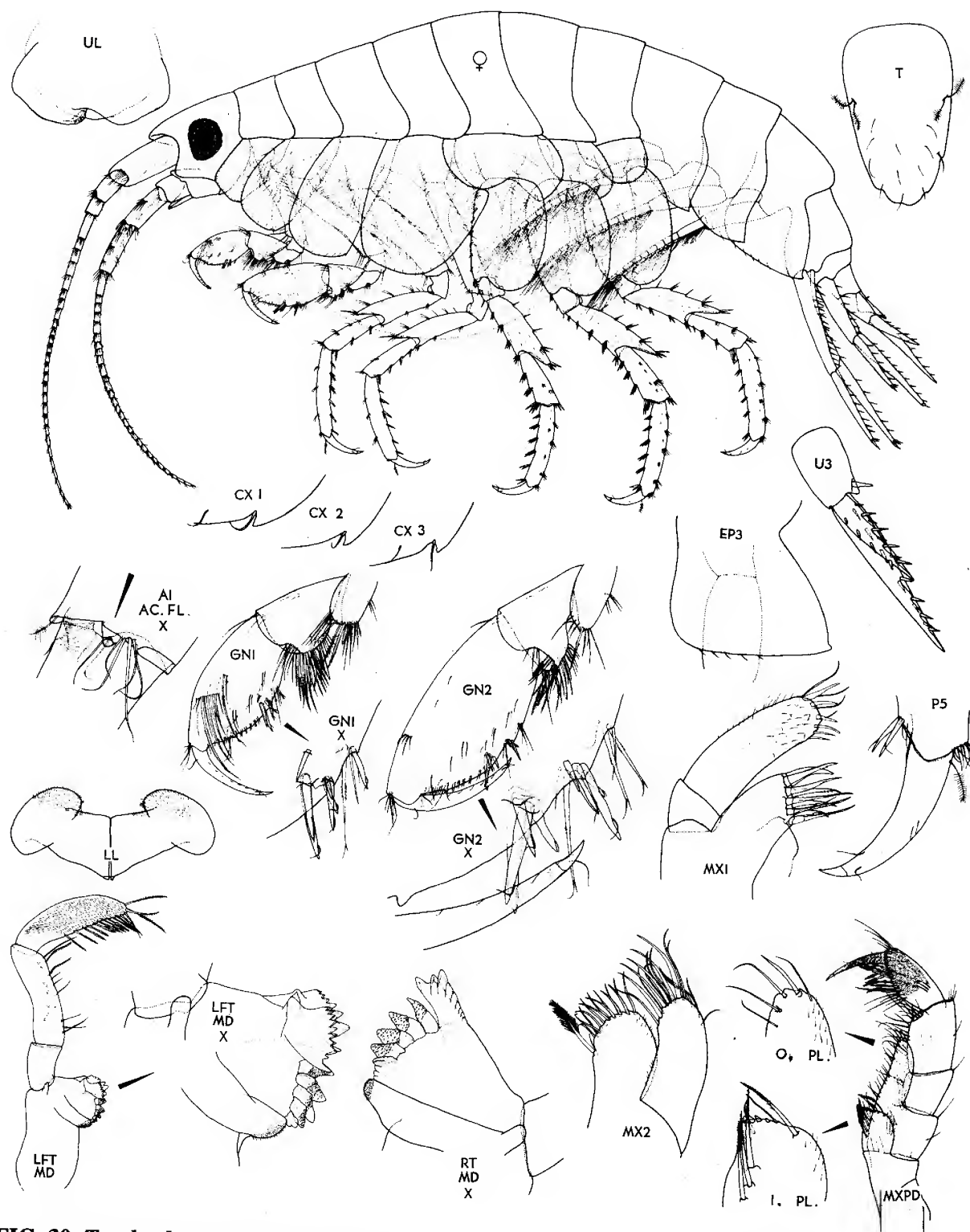


FIG. 30. *Trachypleustes vancouverensis*, n. sp. Female ov (4.5 mm). Cape Scott, Vancouver Island.

- female (5.0 mm), **Holotype** (slide mount), CMN Cat. No. NMCC1995-0084; 2 females, **Paratypes**, CMN Cat. No. NMCC1995-0085. B21b, Off Brady's beach, 10-20 m naturalist's dredge, algae, debris over sand, June 1 - 3 females (1 slide mount). Off Edward King I., from sponge, W. C. Austin Stn. 101/76 - 1 male (slide mount), 2 females.

Race Rocks, Vancouver I., LW level, Anita Voss coll., April 25, 1986 - 1 male (slide mount) + ~40 other specimens.

WASHINGTON-OREGON

Coastal localities. ELB Stns., July-August, 1966: W40, Mukkaw Bay at Sooes Pt. - 2 females, 12 male (slide mounts); W58, Seal Rock - 1 male (slide mount).

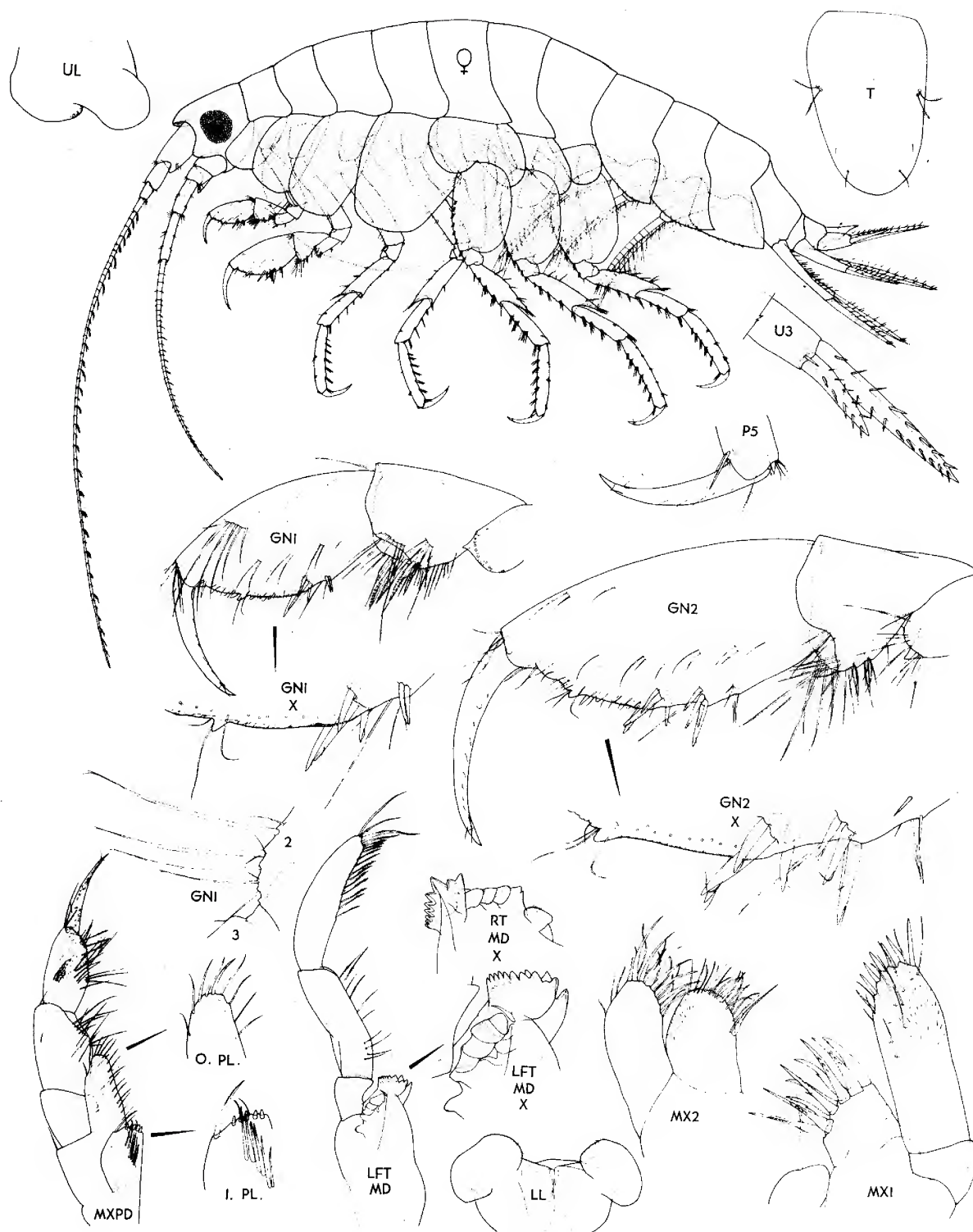


FIG. 31. *Trachypleustes trevori*, new species. Female ov (5.0 mm). Trevor Channel, B. C.

Diagnosis. Female ov. (5.0 mm): Head, rostrum short, little exceeding lateral process; eye nearly round. Antenna 1 much longer than antenna 2; peduncular segment 1 not exceptionally large, length slightly longer than segments 2 & 3 combined; flagellum with ~42 segments, alternately with aesthetascs. Antenna 2, peduncular segments 4 & 5 relatively short, slender; flagellum with ~38 short segments, each with whorl of short setae.

Lower lip, inner lobes relative narrow and deep. Mandible, molar minute much smaller than blades; spine row with 4-5 very short, thick, flat, pavementlike blades; cutting edge of incisor with 9-10 uneven teeth, smallest distally; palp segment 3 narrowing gradually, inner margin with 12 slender pectinate "D" spines; left lacinia broad, deep, cutting edge with 10 uneven teeth. Maxilla 1 palp cylindrical, obliquely rounded apex with 7 slender spines. Maxilla 2,

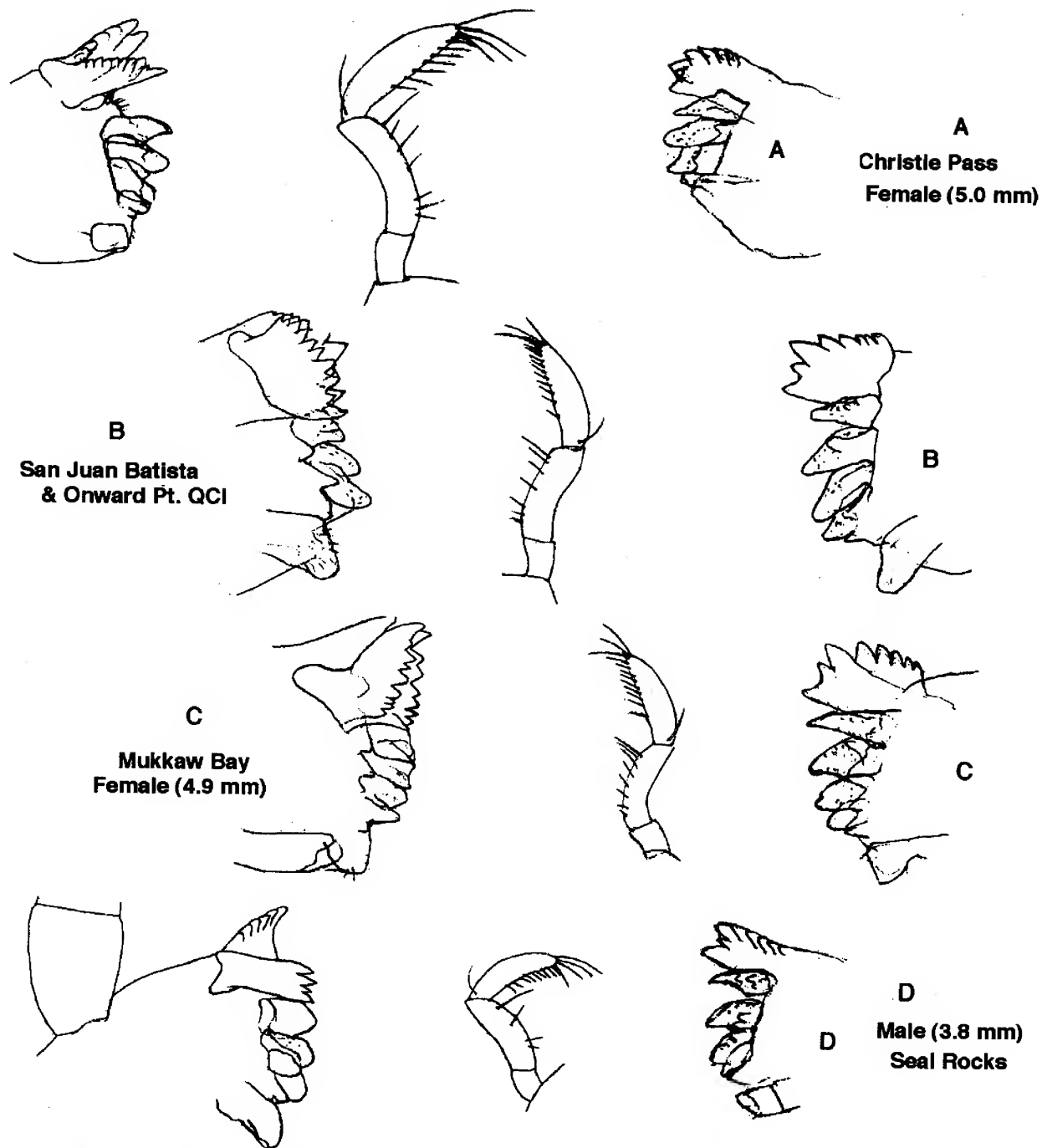


FIG. 32. *Trachyleustes trevori*, new species. A.-D locations; variations in mandibular blades & palp.

outer plate regular. Maxilliped, inner plate with 6 inner marginal setae and 4 apical marginal "button" spines; outer plate, apex narrowly rounding, with singly slender spine; palp ordinary.

Coxae 1-3 medium, relatively shallow, hind corners each with single small cusp. Gnathopod 1, propod much smaller than propod of gnathopod 2; proximal spine group at postero-distal angle with 2 spines; hind margin smooth, lacking spines or setae. Gnathopod 2, carpal lobe lacking pectinate setae; propod with proximal group of four spines at postero-distal angle; hind margin with distal cluster of short simple setae.

Peraeopods 3 & 4 ordinary, slender; segment 4, anterior margin weakly setose; dactyls medium. Peraeopods 5-7, bases not exceptionally broad, increasing posteriorly; segments 4-6, margins with clusters of short spines; segment 5 not shorter than 4; dactyls medium, curved.

Pleon plates 1 & 2, hind corners acuminate; pleon plate 3, hind corner squarish. Urosome 2, dorsal margin nearly occluded by segments 1 & 3. Uropods 1 & 2 long, slender, margins of rami strongly serially spinose. Uropod 3, outer ramus short, length $\sim 1/2$ slender inner ramus having 7-8 pairs of marginal spines.

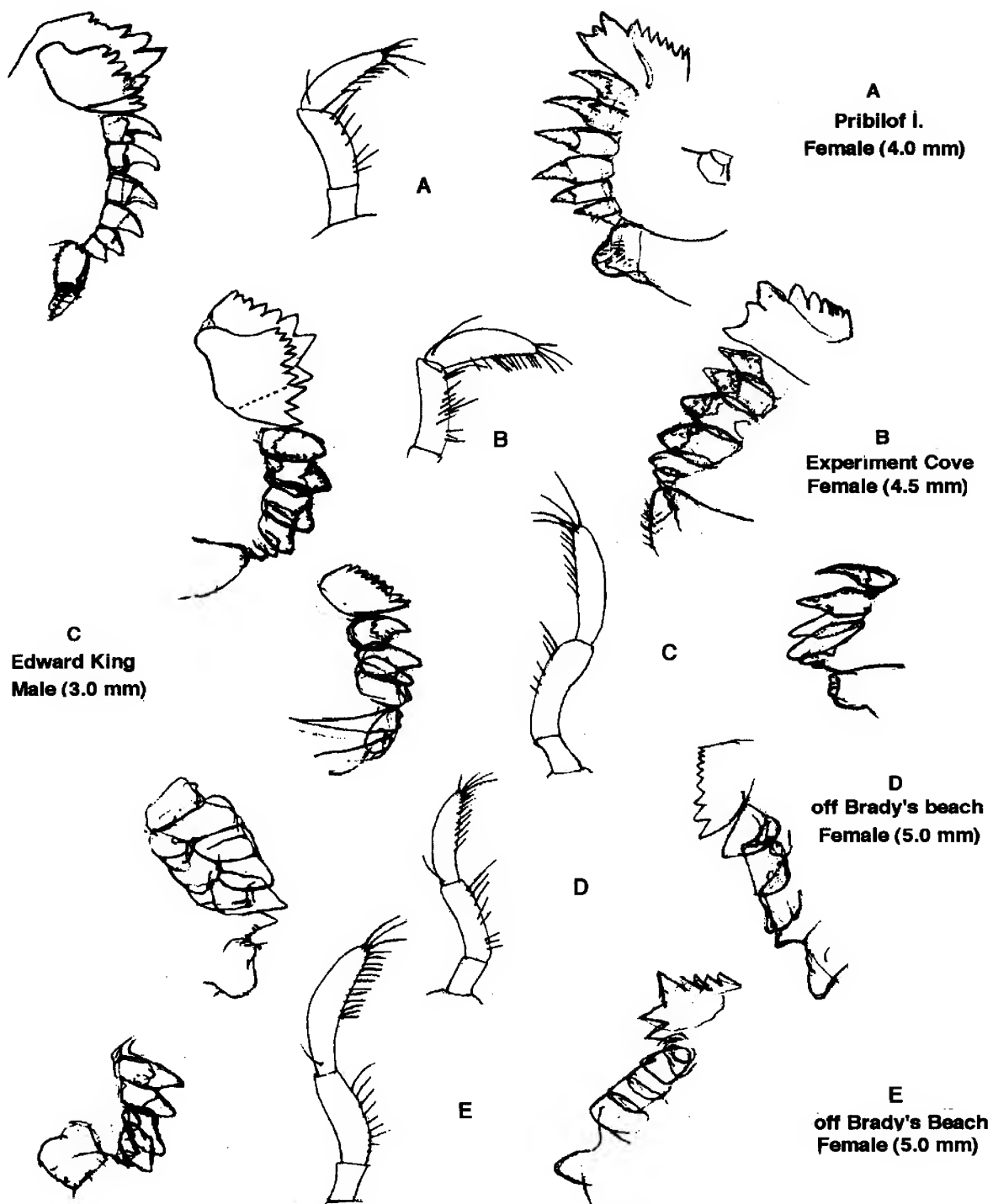


FIG. 33. *Trachypleustes trevori*, new species. A-E locations. Variations in mandibular blades & palp.

Telson ordinary, apex smoothly rounded. Coxal gills on pereopods 4-5 short, saclike

Etymology. The species name alludes to the type locality in Trevor Channel, Vancouver Island, British Columbia.

Distributional ecology. The species ranges from southeastern Alaska, commonly throughout British Columbia to central Oregon, along exposed rocky coasts, associated with sponges and tunicate in under-rock habitats at LW level.

Taxonomic commentary. Material from the following stations are presently considered variants of *T. trevori*. This treatment is not entirely satisfactory, since "variants" may prove to be specifically distinct when more extensive material can be studied:

T. rachypleustes (small-eyed variety, Fig. 32D) having only 3-4 "pavement blades", at Stns. A175; H14a: W40; W58. *T. rachypleustes* (northern variety, Fig. 33A) having 5-6 thick, acute blades, palp with 6-7 pectinate spines, from the Pribilof Islands, Bering Sea.

***Micropleustes*, new genus**

Parapleustes Barnard, 1969a: 425 (partim).—Ishimaru, 1984: 432 (partim).—Barnard & Karaman, 1991: 649 (part).

Type species. *Parapleustes nautilus* J. L. Barnard 1969b: 199.

Species composition. *Micropleustes behningi* (Ishimaru, 1984); *M. behningioides*, new species; *M. longimanus* (Ishimaru, 1984); *M. nautiloides*, new species.

Diagnosis. Body small, smooth to slightly rugose above. Head, rostrum very short; head lobe subacute; inferior antennal sinus elongate, shallow. Eyes small, roundish. Antennae short, subequal, flagella little longer than respective peduncles, weakly setose; accessory flagellum minute. Antenna 1 slightly the longer in male.

Mouthparts somewhat modified. Upper lip shallowly and submedially notched, lobes slightly asymmetrical. Lower lip wide, inner lobes deep, outer lobes oblique, rounded. Mandible: incisor with few (6-8) teeth; left lacinia 6-9 cusped; blades medium heavy, distally pectinate, 7-9 in number; molar small, apex blunt, weakly setulose; palp segments relatively short, stout; segment 2 with few (3-8) inner marginal setae; segment 3 subequal with few (5-10) inner marginal pectinate setae. Maxilla 1, outer plate with 9 tall apical spine-teeth; inner plate with single apical setae, occasionally lacking; palp segment 2 normal, apex with 4 short spines, segment 1 with 1+ outer marginal setae. Maxilla 2, inner lobe slightly broadened, inner margin often with 2 plumose setae. Maxilliped, segment 3 not conspicuously enlarged, longer than palp segment 1; dactyl strong, palp segment 3 lacking distal process; inner plate with 1-2 stout, apically pectinate inner marginal setae.

Coxal plates large, broad, deep; coxa 1 not broadened or bent forward distally; postero-distal notch minute, often multiple (2-4). Gnathopods small to medium strong, not sexually dimorphic; propod tending to elongation; carpus variable, hind lobe short or lacking; palm of propod shorter than posterior margin, smoothly convex, lacking median tooth, postero-distal angle with 1-2 groups of spines.

Peraeopods 3-7 short, medium stout, normally spinose; segment 5 distinctly shorter than 4; dactyls normal, strong. Peraeopods 5-7 regularly homopodous, bases very broad.

Pleon side plates deep, medium broad, hind corners little produced. Pleopods normal, not sexually dimorphic, rami subequal, slightly longer than peduncles. Urosome short, segment 2 nearly occluded dorsally. Uropods short; rami of uropod 1 and uropod 2 subequal, outer slightly the shorter, sparsely spinose, about equal in length to peduncle. Uropod 3 short, extending less than twice length of telson; outer ramus distinctly the shorter.

Telson elongate, dorso-lateral penicillate setae markedly distal. Coxal gills of two types: anterior two pairs slender, sublinear; posterior three pairs larger, platelike, smallest on peraeopod 6.

Etymology. A combining form of the Greek "mikros" (small) and the root generic name "pleustes", referring to the small body size of component members of the genus.

Distributional ecology. All five species of the genus are endemic to the North Pacific region, three on the Asiatic, and two on the North American coast.

Taxonomic commentary. Within subfamily Parapleustinae, the genus *Micropleustes* occupies a somewhat isolated position. It combines a number of relatively plesio-morphic character states, especially in the mouthparts, with a relatively advanced condition of the antennae, coxal plates, gills, uropods, and telson. In balance, however, the genus is least distant from the type genus *Parapleustes* (p. 127).

Micropleustes nautilus (J. L. Barnard)
(Fig. 34)

Parapleustes nautilus J. L. Barnard, 1969b: 199, fig. 55.—Austin, 1985: 592.—Stauder, 1987: 379, fig. 18.77.—Barnard & Karaman, 1991: 650.

Material examined. About 185 specimens in 44 lots:
ALASKA.

Bering Sea: Attu I., Massacre Bay, C. E. O'Clair coll., June 23, 1972 - 2 females.

Amchitka I., Banjo Pt., Sta. B1G1, C. E. O'Clair coll. Aug. 14, 1971 - 32 specimens incl. males, females, im. (male, female slide mounts); *Ibid.*, Stn. IA-2, plot 28, bedrock reefs uplifted by underground nuclear tests, May 22, 1974 - 2 females.

Southeastern Alaska. ELB Stn. S5B7, 1980 - 1 female.

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns., June-July, 1957: W4a (1); W12 (1); W9a (1); H14 (1).

Northcentral coast. ELB Stns., July, 1964, 1959: H1(4); H33 (8); H39 (2); H44 (~20); H47 (1); N1 (1).

Vancouver I., north end. ELB Stns, July, 1959: O1 (4); O5 (1); 07b (4); O15 (1).

Vancouver I., southern end. ELB Stns., July-August, 1955: F1 (2); P4 (1); P6c (3).

ELB Stns., 1970: P702 (2); P712 (7). ELB Stns., 1975: P3a (2); P5a (2); P5b (2); P5d (3); P20 (2). ELB Stns., 1976: B3 (1); B13 (5); B28 (2). ELB Stns., 1977: B6a (1); B8 (2); B11b (1); B19b (2).

Wizard Inlet, D. Kittle Stn. 712, July 28, 1972 - 1 male, 1 female (fig'd specimen) (slide mounts) + 1 female, 3 im.

Barkley Sound, Broken I. group, C. Lobban coll., July 7, 1971 - 1 female; *Ibid.*, July 9 - 10 specimens. Bordelais I., from sponge at LW level, R. J. Anderson coll., June 26, 1976 - 1 male (slide mount).

WASHINGTON-OREGON.

Coastal localities. ELB Stns., July-August, 1966: W22 (1); W40 (8); W58 (~15); W60 (6).

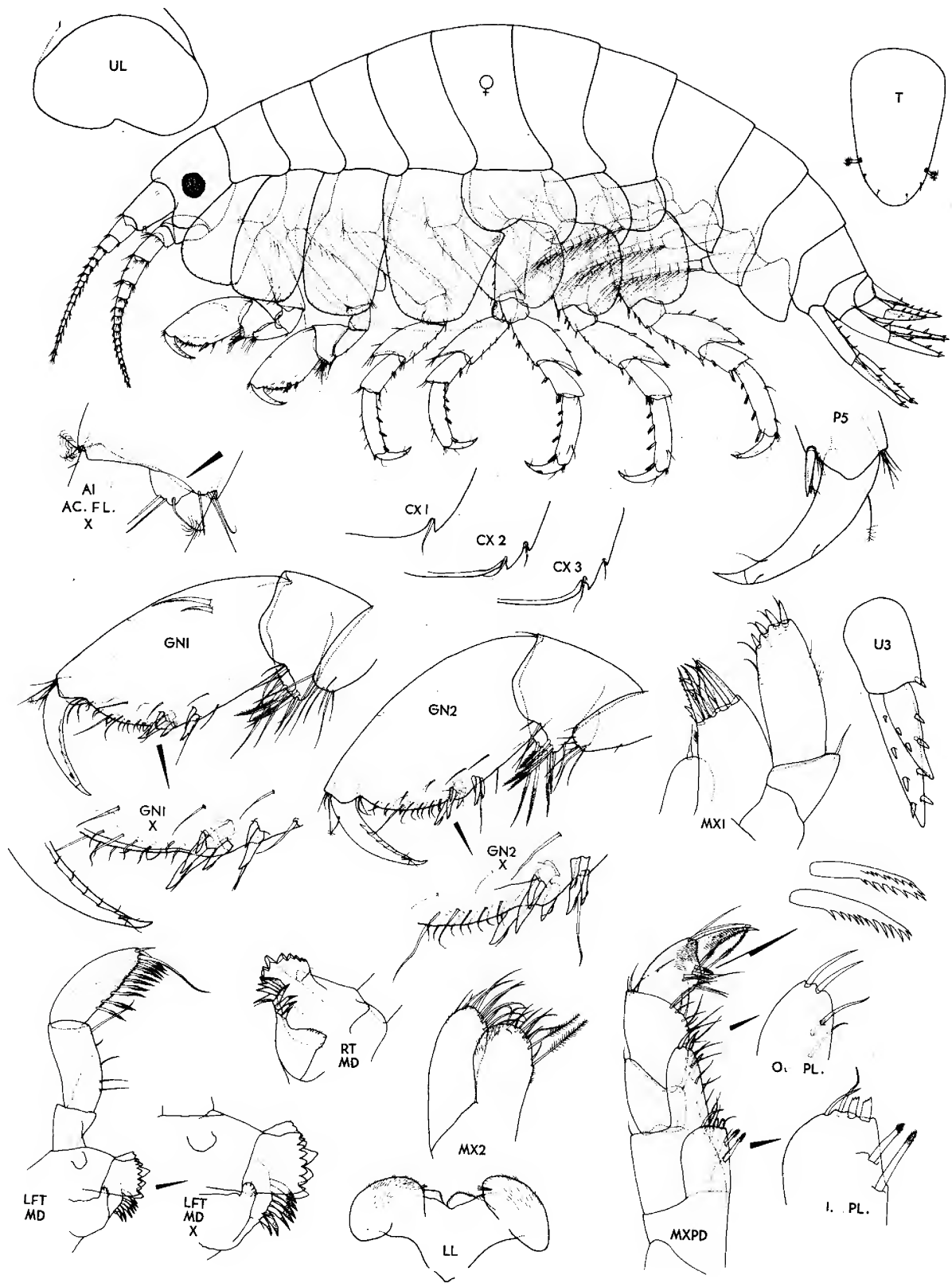


FIG. 34. *Micropleustes nautilus* (J. L. Barnard). Female ov (3.1 mm). Wizard Inlet, B. C.

KEY TO SPECIES OF *MICROPLEUSTES* OF THE NORTH PACIFIC REGION

1. Gnathopods, propod elongate, length of lower margin ~2Xpropod depth; palm of propod short, length less than half that of posterior margin; maxilla 1, inner plate bare; inner ramus of uropods 1 shorter than peduncle 2.
- Gnathopods, propod not elongate, length less than twice depth; propod palm normal, length more than half posterior margin. maxilla 1 inner plate with single apical seta; uropods 1, inner ramus not shorter than peduncle 3.
2. Gnathopod 1, carpus distinctly longer than carpus of gnathopod 2; coxal plates 1-4 only slightly deeper than corresponding body plates; peraeopods 5-7, segment 4 wide, width = length; telson length about twice width, linguiform in shape *M. longimanus* (p. 117)
- Gnathopod 1, carpus about equal to that of gnathopod 2; coxal plates 1-4 very deep, much deeper than corresponding body plates; peraeopods 5-7, segment 4 normal, length distinctly greater than width; telson length about 3 X width, apex narrowly rounding *M. nautiloides*, n. sp. (p. 113)
3. Peraeopod 7, segment 4 postero-distally nearly totally overhanging segment 5 ... *M. behningi* (p. 115)
- Peraeopod 7, segment 4 less broad, postero-distally overhanging segment 5 by 1/2 to 2/3 4.
4. Gnathopods, palm of propod distinctly shorter than posterior margin; postero-distal palmar angles with two distinct groups of spines; telson regularly narrowing distally *M. nautilus* (p. 111)
- Gnathopods, palm of propod about equal in length to posterior margin, postero-distal angle with two tight clusters of spines appearing almost as one group; telson, margins constricted medially *M. behningioides* (p. 116)

Coos Bay, Oregon, K. E. Conlan Stn. 08-23 - 2 females, 8 other specimens.

Diagnosis. Female ov (3.2 mm): Body and coxal plates medium deep. Head, eye round, black. Antenna 1 medium, peduncle 1 large, length > segments 2 & 3 combined; flagellum 14-segmented. Antenna 2, slightly longer than 1, peduncular segment 4 & 5 subequal; flagellum 14-segmented.

Upper lip with broad apical V-cleft; lobes asymmetrical. Lower lip, inner lobes shallow, outer lobes smoothly ovate, oblique. Mandible, molar very small apex rounded; spine row with 7-9 medium, distally pectinate blades; cutting edge of incisor with 7-8 unequal teeth; palp segment 3 with 9 inner marginal pectinate spines and 1 long terminal seta; left lacinia 8-dentate. Maxilla 1, inner plate with single apical seta, palp segment 1 with single "shoulder" seta; segment 2 slightly broadest medially, apex with 4 spines. Maxilla 2, inner plate slightly broadened distally, inner margin with 2 plumose setae. Maxilliped, inner plate with 2 inner marginal spines and 2 apical teeth; outer plate medium, narrowing to rounded apex, with 2 slender curved spines; palp, dactyl slender minutely pectinate, not longer than segment 3.

Coxa 1 broadest distally. Coxa 5, lobes shallow. Gnathopod 1, carpus short, deeper than long; propod short-rectangular, length ~1.5 X depth, with proximal cluster of 2 stout median facial setae; palmar margin short, convex, postero-distal angle with cluster of 5 spines; hind margin nearly straight, with distal cluster of 2 spines; dactyl weakly setulose behind. Gnathopod 2 subsimilar, propod slightly heavier and deeper than in gnathopod 1.

Peraeopods 3 & 4 relatively short and stout, segment 4 slightly broadened; dactyls short. Peraeopods 5-7 closely

homopodous in size and form; bases broad, rounded behind, postero-distal lobe medium deep; segment 4 slender, postero-distal lobe overhanging segment 5 by half its length; dactyls medium, length about 1/2 segment 6.

Pleon plate 3, hind corner not acuminate. Uropod 1 slender, rami subequal, with 1-2 marginal spines. Uropod 2, rami subequal, slightly shorter than peduncle. Uropod 3, outer ramus short, with 3-4 marginal spines, length ~1.5 X each of peduncle and outer ramus.

Telson medium, slightly narrowing distally to rounded apex, penicillate setae distal.

Distribution. From SE Alaska to middle and southern California, intertidal to shallow depths (5 m), associated with under-rock algal and sponge communities.

Taxonomic commentary. Morphological variations were noted in O'Clair material from Alaska, and in ELB material at Stns. P712 and W40, but were not considered significant at the species level.

Micropleustes nautiloides, new species
(Fig. 35)

Parapleustes species "A" J. L. Barnard, 1969b: 203?

Material examined:

BRITISH COLUMBIA.

Southern Vancouver I.: ELB Stn. P712, Off Hanes I., Trevor Channel, under boulders and algal mats, LW level, July 21, 1970 - 4 males, 2 females, 2 im.

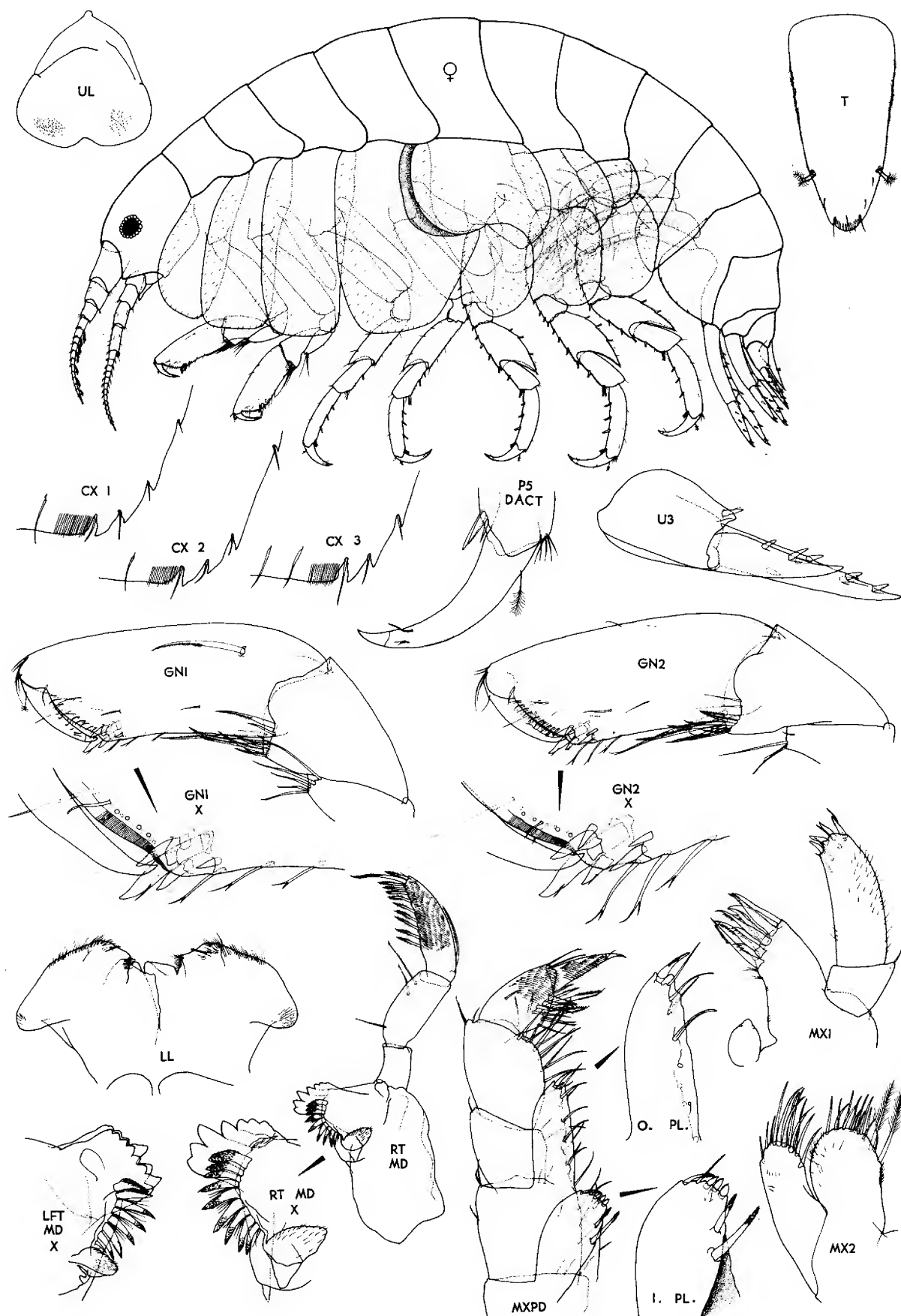


FIG. 35. *Micropleustes nautiloides*, new species. Female ov (2.9 mm). Sunset Bay, Oregon.

WASHINGTON-OREGON.

Coastal Localities. ELB Stn. W40, Mukkaw Bay, at Sooes Pt., from bedrock walls and under boulders, LW level, July 31, 1966 - 9 specimens. Sunset Bay, south of Charleston, Coos Co., K. E. Conlan Stn. 06-06, in *Rhodomela larix*, July 8, 1986 - female (2.9 mm) **Holotype** (slide mount), CMN Cat. no. NMCC1995-0074; *Ibid.*, Stn. 06-03 - 3 females (to 3.1 mm) (1 slide mount), Paratypes, CMN cat. No. NMCC1995-0075; *Ibid.*, Stn. 06-12 - 9 females ov, 3 imm; *Ibid.*, Stn 08-6 - 2 im.

Diagnosis. Female ov (2.9 mm): Body and coxal plates deep. Head small, flat-rounded, black. Antennae short. Antenna 1, peduncular segment 1, length = segments 2 & 3 combined; flagellum 11-segmented. Antenna 2, slender, slightly the longer, flagellum 11-segmented.

Upper lip deep, with narrow apical V-notch; lobes nearly symmetrical. Lower lip inner lobes deep, outer lobes large, oblique. Mandible, molar medium, apex sharply rounded; spine row with 7-9 stout distally pectinate blades; cutting edge of incisor with 7 unequal teeth; palp segment 3 with elongate basal "A" seta, inner margin with 9 pectinate spines; left lacinia 8-dentate. Maxilla 1, inner plate small, lacking apical set; palp segment 1 with single "shoulder seta; palp segment , narrowing, with 4 apical spines. Maxilla 2, inner plate broad, with 2 inner marginal plumose setae. maxilliped inner plate large, narrowing distal with 2 inner marginal spines, and 3 apical marginal short spines; outer plate relatively tall, with single curved spine at subconical apex; dactyl nearly straight, minutely pectinate, not longer than segment 3.

Coxal 1 little expanded distally, hind corner with 3 small cusps. Coxae 2-3, depth ~2X width, hind corners each with 3 small cusps. Coxa 4, width = depth. Coxa 5, lobes deep. Gnathopod 1, carpus longer than deep, hind lobe shallow, short; propod slender, elongate, length ~2X depth, palmar margin short, oblique convex, postero-distal angle with group of 4-5 spines, one distinctly largest; hind margin straight, with distal cluster of 2 short spine and a few cleft-tipped setae; dactyl short, weakly setulose behind. Gnathopod 2 closely subsimilar, propod slightly stouter.

Peraeopods 3 & 4, slender; dactyls medium. Peraeopods 5-7 homopodous; segment 4 relatively short, broad, postero-distal process overhanging 2/3 of short segment 5; dactyls large, length > 1/2 segment 6. Peraeopod 5 slightly shortest; basis broadest, rounded behind; bases of peraeopods 6 & 7 less expanded, hind margin nearly straight.

Pleon plate 3, lower margin convex, hind corner acute, produced. Uropods 1 & 2 rami shorter than peduncle, distally narrowing. Uropod 2, outer ramus distinctly the shorter. Uropod 3 ordinary, inner ramus with 3 marginal spines. Telson elongate linguiform, narrowing to sharply rounded apex; penicillate setae distal.

Distributional ecology. From central British Columbia to southern Oregon, possibly central California, intertidally and immediately subtidal, in algal mats (*Rhodomela*) and

Phyllospadix clumps, of lotic high salinity waters.

Etymology. A combining form of "nautilus" + "oides" in reference to the overall similarity of this species to *Micropleustes nautilus*.

Taxonomic commentary. *Micropleustes nautiloides* is taxonomically closer to *M. longimanus* than to *M. nautilus* (see Fig. 38, p. 118). *Parapleustes* sp. "A" of Barnard (1969b) may be this species.

Micropleustes behningi (Gurjanova)

(Fig. 36)

Neopleustes behningi Gurjanova, 1938: 315, fig. 30.

Pleustes behningi Gurjanova, 1951: 641, fig. 438.

Parapleustes behningi Barnard & Karaman, 1991: 650 (part).—Ishimaru, 1994: 54 (part?).

Parapleustes behningi Ishimaru, 1984: 407, figs. 3-9.

Diagnosis. (mainly after Gurjanova, 1951). Female (1.5 mm): Body and coxal plates short, deep. Head, eye subquadrate, black. Antennae very short. Antenna 1, peduncular segment 1 stout, length ~ 2X segments 2 & 3 combined; flagellum 8-segmented. Antenna 2 stout, slightly the longer; peduncular segment 4 & 5 very short; flagellum 8-segmented.

Upper lip with narrow epistome; labrum, lobes nearly symmetrical. Lower lip broad, shallow, outer lobes ovate, nearly vertical. Mandible, molar short, apex bluntly rounded; spine row with 7-8 uneven blades, distally thick, proximally short, slender; cutting edge of incisor with 6(?) irregular teeth; left lacinia 7-8 dentate. Maxilla 1, inner plate small, with short apical seta; palp slender, segment 1 lacking shoulder seta; segment 2 slender, with 3? apical spines. Maxilla 2, inner plate small, little broadened distally, with single short inner margin plumose seta. Maxilliped, inner plate regular; outer plate short, with 2 curved spines at rounded apex; palp, dactyl stout, slightly longer than segment 3.

Coxae 1-4 relatively deep, narrow. Coxa 1 not expanded distally, hind corner with single stout cusp. Coxa 2, distal margin straight, hind corner with 4-5 distinct cusps. Coxa 4 deeper than broad. Gnathopod 1, carpus short, depth > length; propod medium long, length ~1.5 X depth, palmar margin short, oblique, nearly straight; postero-distal angle with cluster of 3 stout spines; hind margin straight, with distal spine; dactyl strong, minutely setulose behind. Gnathopod 2, somewhat similar, but carpus slightly shorter, hind lobe deeper and narrower than in gnathopod 1; propod more elongate and more slender; length ~ 2X depth.

Peraeopods 3 & 4 slender, margins of segments 4-6 weakly spinose; dactyl strong, > 1/2 segment 6. Peraeopods 5-7 relatively short; bases medium broad, hind margin convex, with 6-8 broad crenulations; segment 4 short, postero-distal process elongate, nearly totally overhanging short segment 5 by 80%; dactyls large.

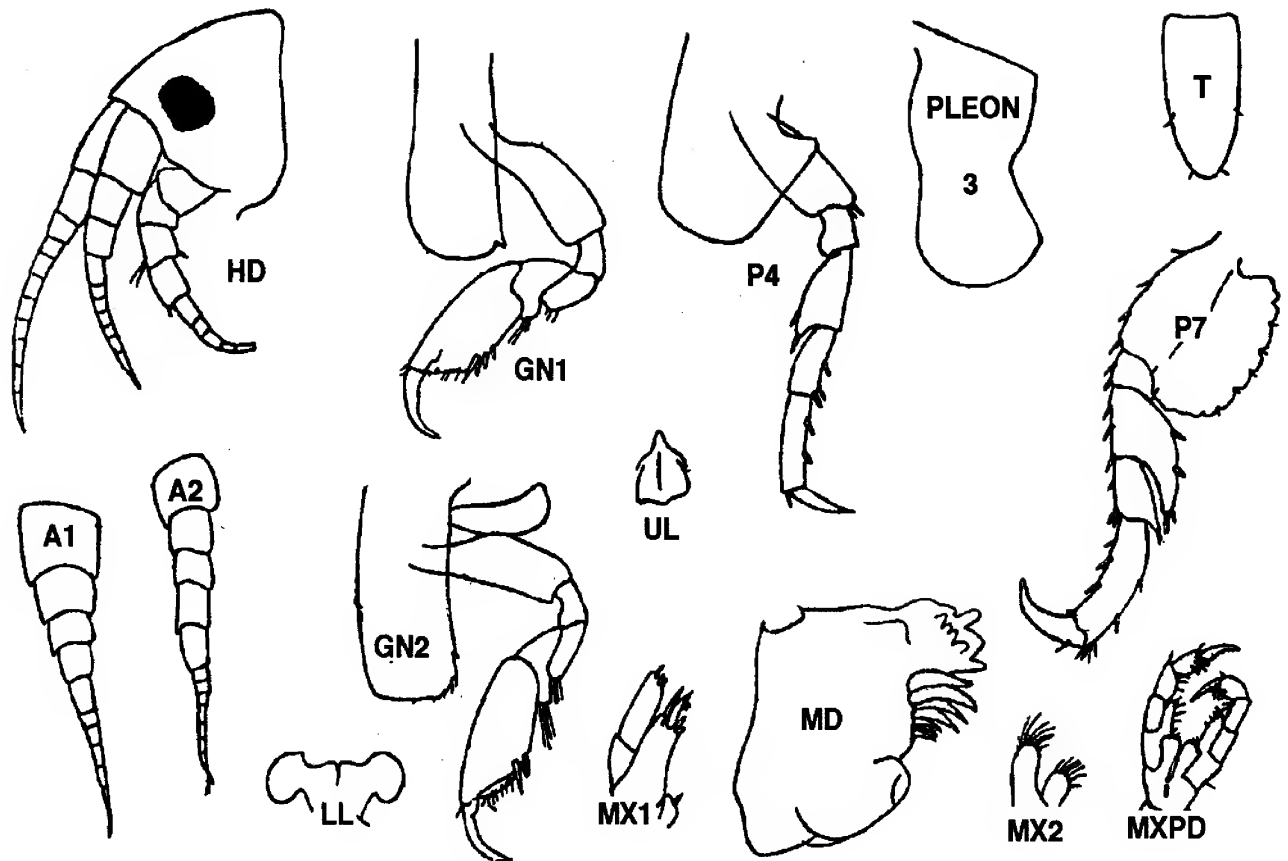


FIG. 36. *Micropleustes behningi* (Gurjanova). Female (4.0 mm). Japan Sea. (after Gurjanova, 1951).

Micropleustes behningioides, new species
(Fig. 37)

Parapleustes behningi Ishimaru, 1984: 407, fig. 4.—Barnard & Karaman, 1991: 650 (part).—Ishimaru, 1994: 54.

Diagnosis. Female (5.9 mm). Body short, compact, coxal plates deep. Head, eye round, medium large. Antenna 1, peduncular segment 1 short < 2 & 3 combined; flagellum long, relatively stout, 19-segmented. Antenna 2 shorter, peduncular segments 4 & 5 short, subequal; flagellum 16-segmented.

Upper lip regular, lobes slightly asymmetrical. Lower lip inner lobes, deep, outer lobes large, oblique. Mandible, molar prominent, slender, apex subacute; spine row with 9 short stout blades; cutting edge of incisor with 8 unequal teeth; palp segment 3 with short, proximal "A" seta, and 10? inner marginal pectinate "D" spines; left lacinia with 7(?) teeth. Maxilla 1, inner plate with single apical plumose seta; palp segment 1 with 2 "shoulder" setae; segment 2, surface finely setulose, apically with 4-5 short spines. Maxilla 2, inner plate short, broadly expanded, inner margin with 2 unequal plumose setae. Maxilliped, inner plate medium, with few distal facial setae, and 4 apical marginal spines; outer plate short, apex narrowly rounded, with 2 slender spines; palp, dactyl stout, nearly straight, not longer than segment 3.

Coxa 1-3 medium broad, deep. Coxa 1 slightly broadened distally, hind corner with 1-2 minute cusps. Coxae 2 & 3, hind corner with 3 minute cusps. Coxa 4 deeper than broad. Coxa 5 lobes deep. Gnathopod 1, carpus short, deep, hind lobe narrow; propod short, length ~1.5X width; palmar margin relatively long, about equal to posterior margin, convex, oblique, postero-distal angle with 3 spines; dactyl minutely setulose behind. Gnathopod 2 subsimilar; carpus slightly shorter and deeper; propod slightly expanding distally.

Peraeopods 3 & 4 stout, 3 distinctly the larger; segment 4 broadened abruptly, with subparallel margins; dactyls medium strong. Peraeopods 5-7 short, subsimilar; bases moderately expanded, hind margins gently convex, minutely crenulate; hind lobes deep; segment 4 broadened, nearly as wide as deep, postero-distal lobe 2/3 overhanging short segment 5; dactyls stout.

Pleon plate 2, hind corner rounded; pleon plate 3 hind corner acuminate. Uropods 1 & 2 short, little or not exceeding uropod 3. Uropod 1, rami and peduncle subequal in length. Uropod 2, outer ramus distinctly the shorter. Uropod 3, outer ramus shorter, length barely 1/ inner ramus.

Telson slender, "pinched" medially, narrowing to rounded apex; penicillate setae distal.

Etymology. A combining form of the species name "*behningi*" and the suffix "*oides*", like the regionally co-occurring species *M. behningi* (Gurjanova, 1938).

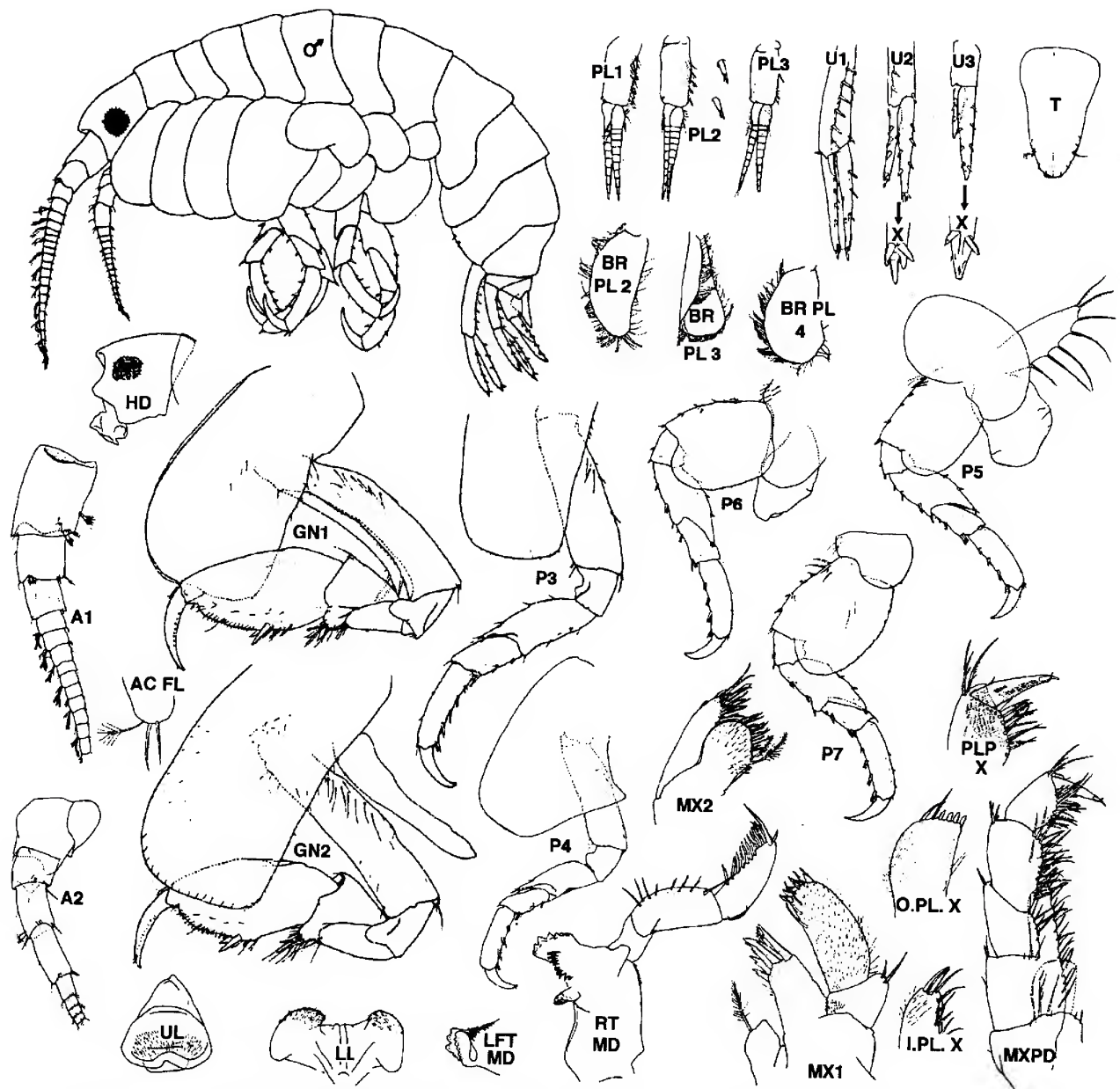


FIG. 37. *Micropleustes behningioides*, new species. Female (5.9 mm); male (4.0 mm). Japan Sea. (after Ishimaru, 1984).

Pleon plate 3 strongly convex below, hind corner obtuse. Uropods 1-3 regular. Telson elongate, narrow, apex sharply rounded; penicillate setae nearly median.

Type material. Ishimaru, 1984, figs. 3-7: Female "a" (5.9 mm), **Holotype**, Samani, Hokkaido; *Ibid.*, fig. 8: Male "e" (4.0 mm), **Allotype**, Oshoro, Hokkaido. Collections of the Faculty of Science, Hokkaido University.

Distribution. Eastern Sea of Japan and southern Hokkaido, among *Phyllospadix* and *Sargassum*, LW-0.5 m depth.

Taxonomic commentary. *Micropleustes behningioides* is readily separable from *M. behningi* (Gurjanova, 1938), and appears morphologically closer to *M. nautilus* (see key, p. 113; also fig. 34, p. 112).

Micropleustes longimanus (Ishimaru)
(Fig. 38)

Parapleustes longimanus Ishimaru, 1984: 438, figs. 25-28.
—Barnard & Karaman, 1991: 650.—Ishimaru, 1994: 54.

Diagnosis. Female (2.9 mm): Body short, compact, coxal plates medium deep. Antennae short, slender, subequal. Antenna 1, peduncular segment 1 short, length < segments 2 & 3 combined; accessory flagellum broadly conical, with 4 apical setae; flagellum 8-segmented. Antenna 2, peduncular segments 4 & 5 slender, subequal; flagellum 8-segmented.

Upper lip shallowly V-cleft apically, lobes nearly symmetrical. Lower lip, inner lobes deep, outer lobes small ovate, oblique. Mandible, molar process, short, conical;

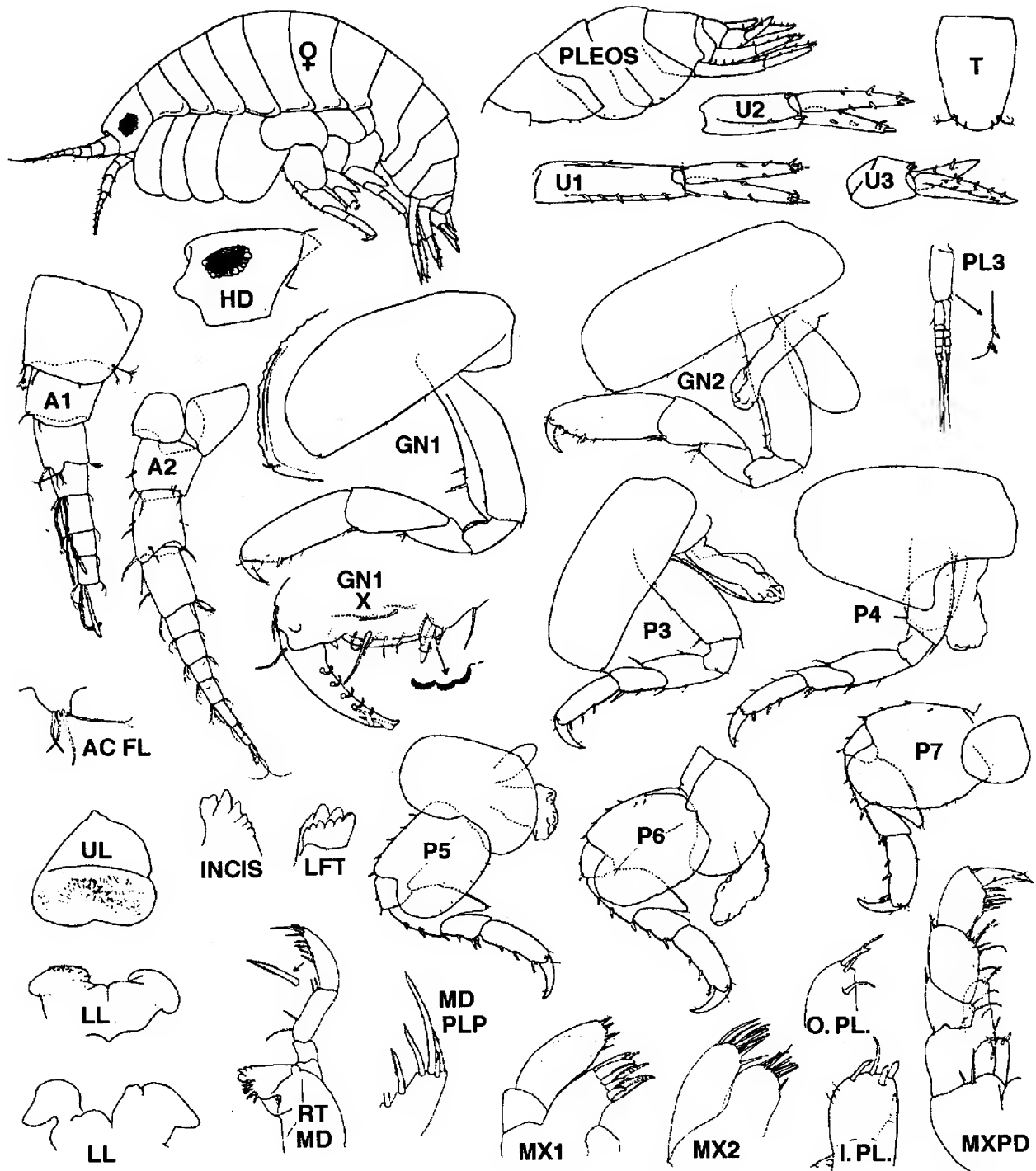


FIG. 38. *Micropleustes longimanus* (Ishimaru). Female (2.9 mm). Japan. (after Ishimaru, 1984).

spine row with 6-7 short blades; cutting edge of incisor with 6-7 unequal teeth; palp segment 3 with 5 inner marginal pectinate "D" spines; left lacinia 6-7-dentate. Maxilla 1, inner plate small, lacking apical seta; palp segment 1 lacking "shoulder" seta; segment 2 narrowing distally, apex with 3-4 slender spines. Maxilla 2, inner plate slightly shorter than outer plate, little broadened, with 1 short inner marginal plumose seta. Maxilliped, inner plate very short, with 1 inner

marginal stout seta, apex with 2 stout and 2 slender spines; outer plate very short, subtruncate apex with 2 slender spines; palp, dactyl curved shorter than segment 3.

Coxae 1-4, lower margins rounded. Coxa 1 slender, hind corner with single small cusp. Coxae 2-3, lower border minutely crenulate, hind corner with single cusp. Coxa 4 deeper than wide. Coxa 5, lobes deep. Gnathopod 1, carpus slender, hind lobe very small, length ~2X depth; propods

slender, length ~3X depth, margins subparallel, palmar margin very oblique, very short, postero-distal angle with single cluster of 3 spines (one large); dactyl short, inner margin with 5 short curved setules. Gnathopod 2 subsimilar, except carpus and propod slightly shorter and deeper.

Peraeopods 3 & 4, segments 4-6 relatively stout, 4 not broadened; dactyl medium. Peraeopods 5-7 very short, closely subsimilar; bases broad, lower hind lobes very deep, hind margins gently convex; segment 4 expanded, broader than deep, postero-distal lobe nearly totally overhanging short segment 5; segment 6 stout, with 2 anterior marginal spines; dactyl medium.

Pleon plate 3, hind corner squared. Pleopods, peduncles stout, outer margins short-spinose; rami short, 12-segmented. Uropods 1 & 2 slightly exceeding uropod 3. Uropod 1, rami subequal weakly marginally spinose. Uropod 2, outer ramus slightly the shorter. Uropod 3, outer ramus short, length ~60% inner ramus. Telson short, slightly narrowing distally to broadly rounded apex; penicillate setae marginally subapical.

Distribution. The species is known from inshore shallows of the mainland and Japanese coast of the Sea of Japan.

Taxonomic commentary. *Micropleustes longimanus* is distinctive in nearly every character state, but in balance appears closest to *M. nautiloides* of the North American Pacific region.

Dactylopleustinae, Bousfield & Hendrycks

Dactylopleustinae Bousfield & Hendrycks, 1994: 38.

Type Genus. *Dactylopleustes* Karaman & Barnard, 1979, monotypy.

Diagnosis. A monotypic group of primitive but secondarily specialized commensal and/or parasitic pleustids.

Rostrum short. Eyes large, reniform. Antennae short, pediform. Accessory flagellum minute.

Upper lip, notch shallow, lobes only slightly asymmetrical. Lower lip with deep, distinct inner lobes. Mandible, molar rounded, non-triturating; palp segment 2 short, segment 3 swollen, lacking baso-facial ("A") setae; right lacinia lacking; Maxilla 1, outer plate short, wide, with 9-16 pectinate spine-teeth; inner plate with 1 apical seta; palp large, terminal segment broad. Maxilla 2, plates short, subequal. Maxilliped, plates small, weakly armed; palp segments short; dactyl pectinate.

Coxae 1-4 deep, 1 shortest. Gnathopods with elongate carpus and propod, longer in gnathopod 2; palmar margins short, lacking median tooth, hind margin setose.

Peraeopods 3-7 short; dactyls short, inner margins finely crenulate or pectinate. Peraeopods 5-7 basically homopodous; coxae regularly and strongly postero-lobate; bases broad.

Pleon plates regular, unmodified. Urosome 2 not oc-

cluded dorsally. Uropods 1 & 2 broad-lanceolate, rami subequal, broad-lanceolate. Uropod 3 medium, rami unequal. Telson keel proximally.

Coxal gills saclike on peraeopods 2-4, plate-like on 5 & 6.

Taxonomic commentary. This monotypic group (consisting to date of three species in one genus) was formerly assigned to the genus *Parapleustes* based on the non-triturating molar and ordinary form of the maxillipedal palp. However, the unusual mixture of plesiomorphic and apomorphic character states justified elevation of the genus *Dactylopleustes* to subfamily ranking (Bousfield & Hendrycks, 1994).

Dactylopleustes Karaman & Barnard

Parapleustes Tzvetkova 1975: 121 (part).

Dactylopleustes Karaman & Barnard, 1979: 112.—Barnard & Karaman, 1991: 647.

Type species. *Parapleustes echinoicus* Tzvetkova, 1975, original designation

Species. *Dactylopleustes echinoides*, new species (p. 121); *D. (Apodactylopleustes) obsolescens* Hirayama, 1988.

Diagnosis. Body small, smooth above, lysianassiform; coxae deep, legs short. Head, rostrum short, about equal to broadly rounded anterior head lobe; inferior antennal sinus shallow. Antenna 1 not longer than antenna 2, segment 2 short, segment 3 very short, flagellum shorter than peduncle; Antenna 2, flagellum shorter than peduncle.

Mouthparts highly modified. Lower lip, inner lobes tall, outer lobes large, oblique to nearly horizontal. Mandible, molar forming a smoothly rounded protuberance beneath 6-8 slender blades; left lacinia with 6-7 rounded teeth; palp slender; segment 1 short, segment 2 weakly setose; segment 3 with few pectinate inner marginal setae. Maxilla 1, outer plate short, broad, apical spines slender, innermost strongest. Maxilla 2, outer plate with heavy spinelike apical setae. Maxilliped, plates weakly armed; inner plate lacking distal "button" spines, outer plate, inner margin concave, apex weakly spined; palp short, segment 2 shortest, segment 3 longest, with medio-distal row of spines; dactyl slender.

Coxal plates 1-4 very deep, broad, much deeper than body plates; coxa 1 distinctly smallest, but not expanded distally; hind cusps 2-5 per plate, small. Gnathopods small, short, subequal, subsimilar, non sexually dimorphic; bases slender, anterior margin setose (more strongly in Gnathopod 1); merus rounded distally; carpus shallow-setose behind, length about equal to propod; palm very short, convex, with few short spines at postero-distal angle, long hind margin with groups of pectinate setae; dactyl short, smooth.

Peraeopods 3-7 short, segmental margins short-spinose; dactyls very short, body heavy, inner margin nearly straight, micro-crenulated. Peraeopods 5-7 regularly homopodous, coxae very deep, hind lobes rounded below; bases broad,

KEY TO SPECIES OF *DACTYLOPLEUSTES*

1. Eyes large, deep, reniform; mandibular palp, segment 2 distinctly longer than segment 1; coxa 1 distinctly shorter than coxa 2; telson elongate; uropods 1 & 2 not modified 2.
 —Eyes medium, ovate, few large facets; mandibular palp slender, segment 2 little longer than 1; coxa 1 slightly shorter than coxa 2; uropods 1 & 2 (male), inner ramus short, broad, weakly armed
 *D. (Apodactylopleustes) obsolescens* (p. 123)
2. Maxilla 1, outer plate with 9 apical spine teeth; peraeopod 5, basis with angular postero-distal lobe; mandibular palp, segment 3 broad, with 7 inner marginal pectinate setae; maxilliped palp, segment 2 subequal to 1, dactyl thick, tip pectinate; gnathopod bases nearly bare of setae . *D. echinoicus* (p. 120)
 —Maxilla 1, outer plate with 15 slender apical spine-teeth; peraeopod 5, basis smoothly rounded behind; mandibular palp, segment 3 slender, with 5 inner marginal setae; maxilliped palp, segment 3 shorter than either 1 or 3, dactyl slender, acute, not conspicuously pectinate; gnathopods 1 & 2, basis strongly setose anteriorly *D. (Neodactylopleustes) echinoides* (p. 121)

evenly rounded behind.

Pleon side plates medium deep, broad, smooth below, hind corners acuminate. Pleopod peduncles short, rami with reduced numbers of segments, not sexually dimorphic. Uropods 1 & 2 short, stout; rami suramceolate, margins serially spinose, tips not spinose. Uropod 3, peduncle short, stout, rami broad-lanceolate, inner ramus distinctly the larger.

Coxal gills largest on peraeopods 4 & 5, smallest on peraeopod 6.

Taxonomic commentary. The three component species of the genus are sufficiently distinct to justify separate generic status. Although Hirayama (1988) recognizes *D. obsolescens* as a distinct subgenus, *Apodactylopleustes* (see key above), further subdivision must await analysis of more extensive material in which new taxa are anticipated.

Dactylopleustes echinoicus (Tzvetkova)
(Fig. 39)

Parapleustes echinoicus Tzvetkova, 1975:122, fig. 1.

Dactylopleustes echinoicus Karaman & Barnard, 1979: 112.—Barnard & Karaman, 1991: 647.

Diagnosis. Female (5.0 mm): Head, rostrum small, shorter than lateral lobes. Eyes moderate, reniform, black. Antennae short, 1<2; segments of the peduncle and flagellum shortened and broad. Flagellum of antenna 1 of 8 segments, of antenna 2 of 5 segments.

Upper lip, lobes slightly asymmetrical. Mandible, spine row with 12 slender short blades; incisor 7-dentate; palp strong; segment 3 longest, with 7 inner marginal pectinate "D" spines. Maxilla 1, palp segment 2 with 5 apical spines, segment 1 lacking shoulder seta. Maxilla 2, plates subequal. Maxilliped, inner plate with 3 apical button spines; outer plate short, with stout apical spine and slender seta; palp segment 3 slender, dactyl short, broad, with apical inner marginal pectinations.

Coxal plates 1 and 2 rectangular, lower margin convex, hind corner with 2 cusps. Coxal plate 4 deeper than broad.

Gnathopod 1 weakly subchelate; basis slender, bare; carpus and propod slender, subequal; hind margin of propod with 3 groups of setae. Gnathopod 2, segment 5 lacking hind lobe, segment 6, hind margin strongly setose, palm very short, oblique, dactyl short.

Pereopods 3 & 4, segment 5 < 4, hind margins with short spines; dactyl short, body with 5-6 prominent posterior pectinations, unguis slender, curved. Peraeopods 5-7, coxae relatively deep; bases expanded to different degrees, 5 sharply angled behind, 7 very broad, rounded, smooth behind; segment 5 shorter than 4; dactyls with small marginal pectinations.

Pleon plates 1-3, hind corner slightly acuminate. Uropod 3 stout, rami broad; inner ramus almost equal to peduncle slightly longer than half outer ramus; outer margin of the outer ramus bare, inner margin with 4 spines.

Telson short almost parallel-sided; apex rounded, unarmed.

Distributional ecology. Known only from Bering Island (Commander Islands, off the east coast of Kamchatka), reef south of Nikol'skoye village.

D. echinoicus is an obligate symbiont of the sea urchin *Strongylocentrotus polyacanthus*. The peraeopod dactyls are modified for holding the crustacean onto the body of the sea urchin, as if "wedged in", and to move around the movable spines on the surface of the test.

Taxonomic commentary. *Dactylopleustes echinoicus* is phylogenetically more primitive than the other two species of the genus subsequently described from Asiatic and North American coast (pp. below). The dactyls of this genus are adaptive to a lifestyle of clinging to the spines and surfaces of sea urchin tests. A less sophisticated form of grasping dactyl was noted in *Commensipleustes commensalis* (Shoemaker) (p. 82). In that species, the dactyl and expanded spinose propod of peraeopods 3-7 form a subchelate claw-like mechanism that enables the amphipod to cling to the pleopods of the spiny lobster *Panulirus interruptus*. Such morphological specializations underscore the high degree of adaptive radiation within subfamily Parapleustinae that is associated with a commensal lifestyle.

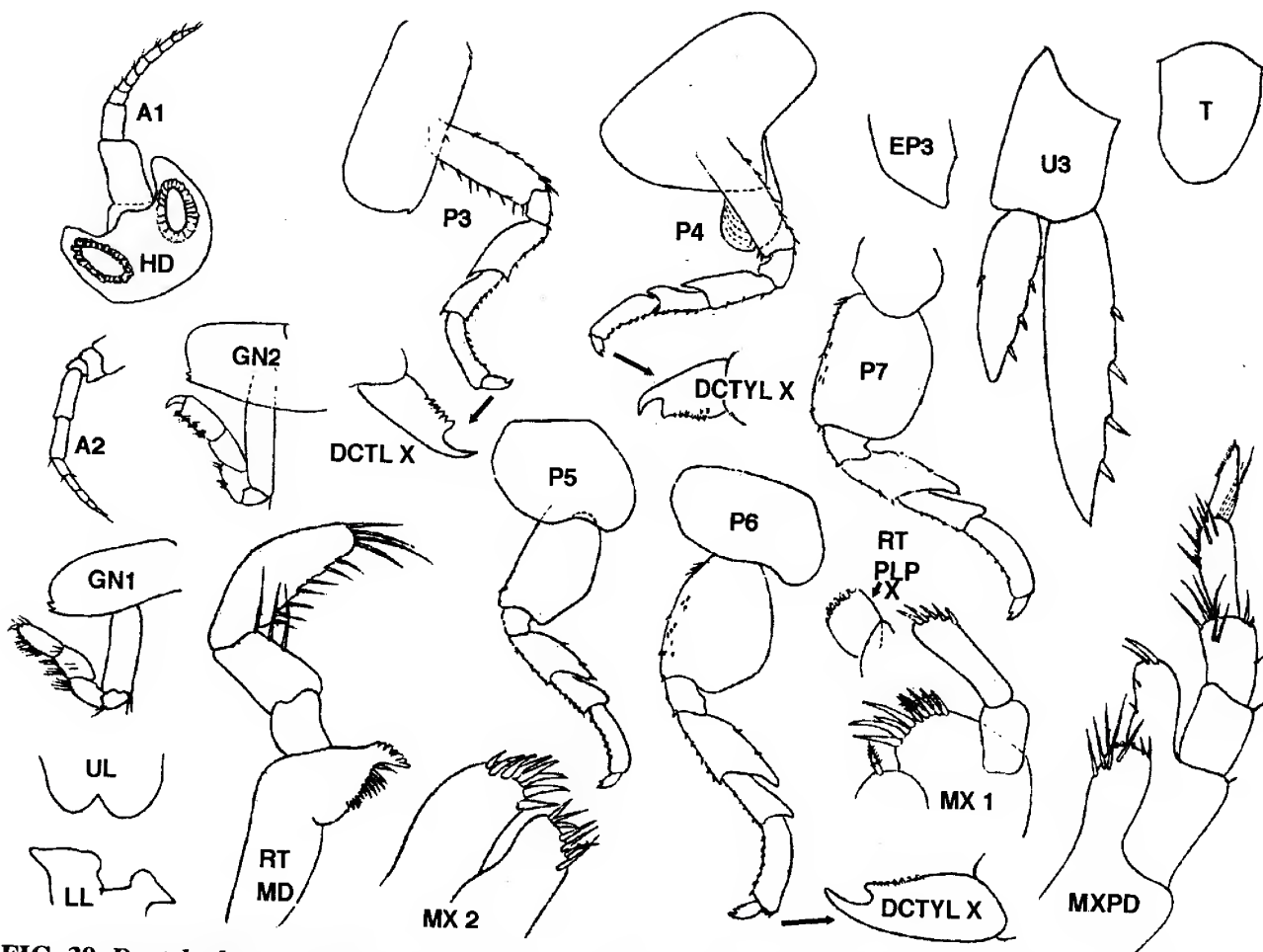


FIG. 39. *Dactylopleustes echinoicus* (Tzvetkova). Female (5.0 mm). Bering Sea. (after Tzvetkova, 1975)

Dactylopleustes echinoides, new species
(Fig. 40)

Dactylopleustes echinoicus Austin, 1985: 592?—Barnard & Karaman, 1991: 647 (part)?.

Material examined.

BRITISH COLUMBIA.

Northern Vancouver I.: ELB Stn. N16, Port Neville, Johnstone Strait., in clumps of *Phyllospadix* and under algal mats, LW level, July 17, 1959 - Female ov (3.3 mm), **Holotype** (slide mount), CMN Cat. no. NMC1995-0079; 3 females, 1 male, **Paratypes**, CMN Catalogue no. NMCC-1995-0080.

Diagnosis. Female ov (3.3 mm): Head, rostrum as long as lateral head lobe. Eye deep reniform, black. Antenna very short. Antenna 1 peduncle 3 not larger than basal flagellar segment, flagellum 5-segmented. Antenna 2, flagellum 5-segmented.

Upper lip, median notch sharp, shallow, lobes nearly equal. Lower lip, inner lobe deep, narrow, outer lobes large nearly horizontal. Mandible molar large, broadly rounded; spine row with 7 slender blades; incisor 8-dentate; left lacinia 8-9 dentate; palp segment 2 relatively long; segment 3 with 4 inner marginal pectinate "D" spines. Maxilla 1, outer plate

with 14 long slender distally curved apical spines; palp broad, with 6 stout apical spines. Maxilla 2, plates short, broad, outer plate with 12 heavy apical spines. Maxilliped inner plate short, apex sloping inward, with 3 minute button spines; outer plate slender, inner margin excavate, apex with 1 heavy spine and 2 setae; palp segment 2 short, 3 with pectinations near base of thin pectinate dactyl.

Coxa 1 distinctly shorter than 2, hind corner with 4 cusps; coxa 2 & 3 with 3 and 2 hind cusps respectively. Coxa 4 very large, subrectangular, deeper than broad. Gnathopod 1, basis, anterior margin strongly setose; propod much shorter and more slender than carpus, with 1 stout distal facial cluster of setae; palm very short, oblique, overhung by stout dactyl. Gnathopod 2, basis less strongly setae; carpus longer, propod subrectangular, palm distinct, strongly convex, nearly vertical, hind margin with 3 setal clusters.

Peraeopods 3 & 4, margins of bases lined with short setae; dactyls short, stout, inner margins with 10+ minute pectinations. Peraeopods 5-7 closely homopodous, bases broadly rounded behind; segment 4 widening distally; segment 5 short; dactyls short, finely pectinate. Coxa 6 deep behind.

Pleon plate 3, hind corner produced, acuminate. Uropod 1 & 2 stout, rami basal broadly nearly as long as peduncle, margins strongly spinose. Uropod 3, inner ramus heavy,

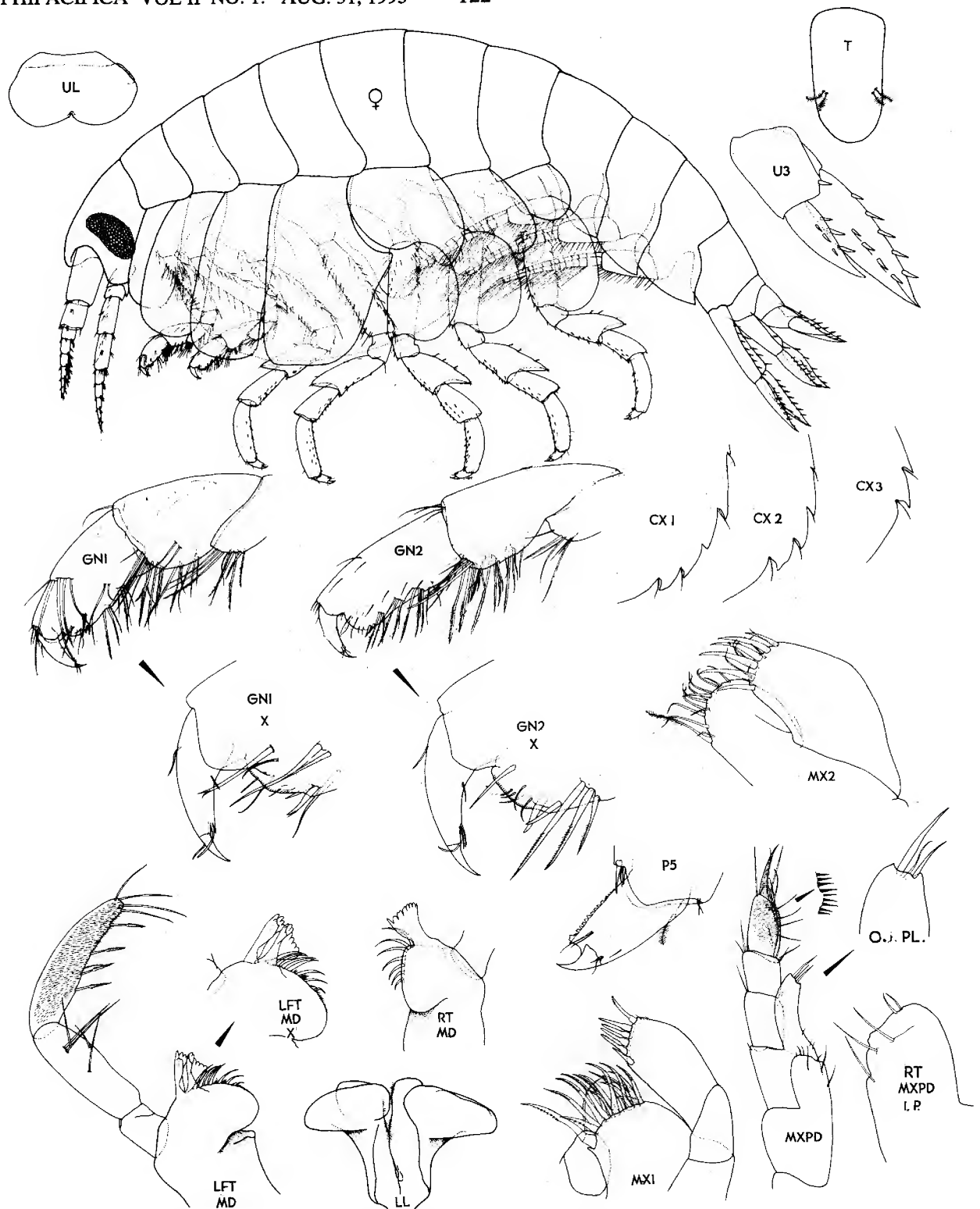


FIG. 40. *Dactylopleustes echinoides*, new species. Female (3.3 mm). Port Neville, B. C.

thick, margins with 4-5 spines; outer ramus with 3 spines on each margin.

Telson relatively long, length 2X width, apex smoothly rounding.

Etymology. Combining the suffix "oides" - like, or similar to, the type species *D. echinoicus*.

Taxonomic & distributional commentary. The host echinoid has not been determined precisely. However, the sea urchin *Strongyocentrotus purpuratus* occurred commonly at the type locality. The echinoid fauna of the region is diverse (Ricketts & Calvin, 1968) and would indicate that several other host-specific species of *Dactylopleustes* may yet be discovered in the North American Pacific region.

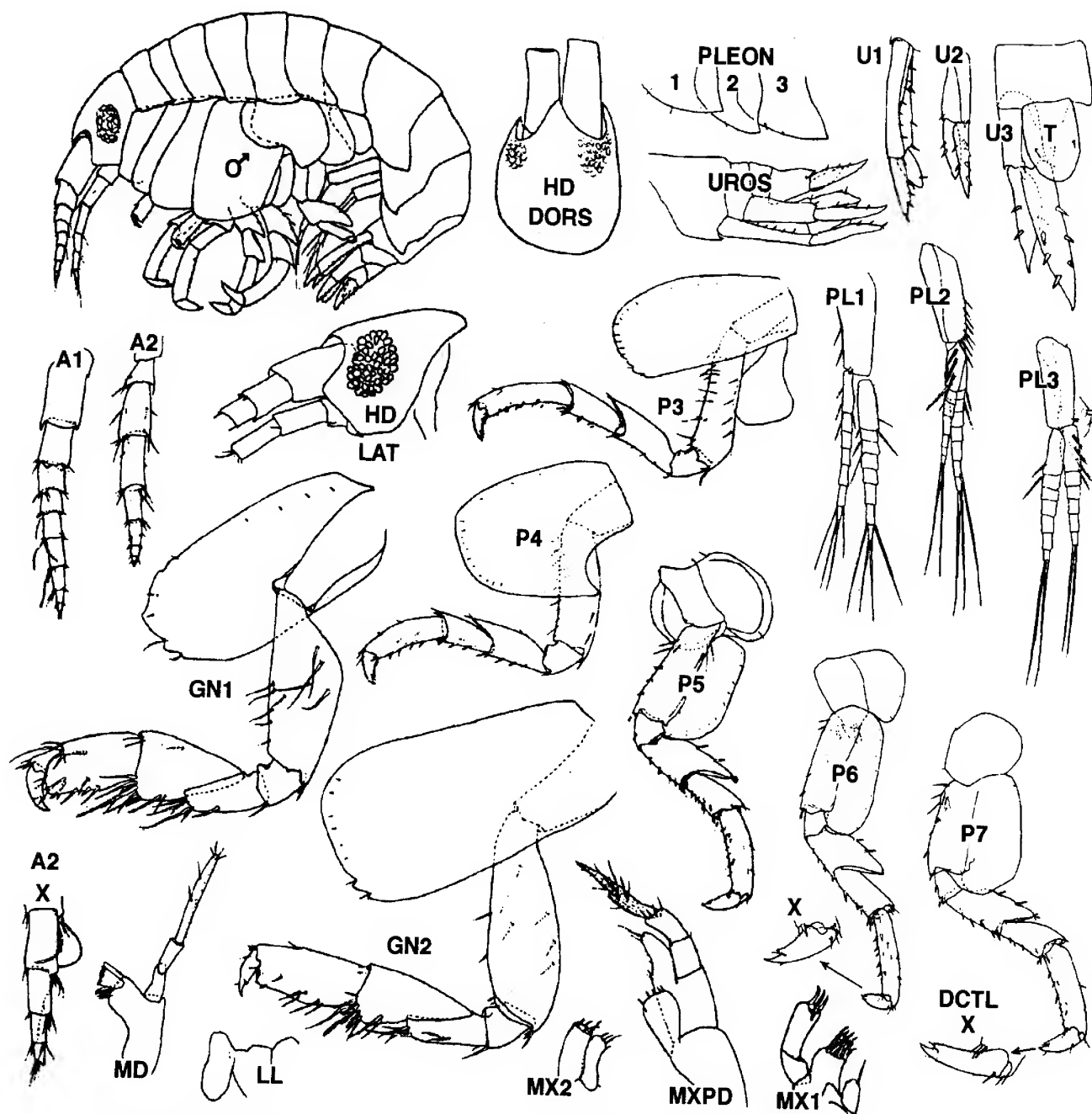


FIG. 41. *Dactylopleustes obsolescens* Hirayama. Male (2.0 mm). Ariake Sea. (after Hirayama, 1988).

Dactylopleustes obsolescens Hirayama
(Fig. 41)

Dactylopleustes (*Apodactylopleustes*) *obsolescens*, Hirayama, 1988: 44, figs. 269-271.—Ishimaru, 1994: 54.

Diagnosis. Male? (2.0 mm): head, rostrum equal to lateral head lobes. Eye oval, large, orange. Antennae relatively long. Antenna 1, peduncular segment 3 larger than adjacent flagellar segment; flagellum 6-segmented. Antenna 2, peduncular segments 4 & 5 slender, subequal; flagellum 5-segmented.

Lower lip, outer lobes nearly vertical. Mandible, molar

process evanescent spine row with 5 short blades; incisor 7-8 dentate; left lacinia 8-9 dentate; palp segment 2 very short; segment 3 long and slender with 1-2 inner marginal pectinate "D" spines. Maxilla 1, outer plate with 11 apical spines; palp, terminal segment apically truncate, with 5 spines. Maxilla 2, outer plate much the stouter, with 3-5 apical spines. Maxilliped, inner plate apically truncate, lacking button spines; outer plate slender, inner margin excavate; palp segment 2 short, distally pectinate, dactyl pectinate.

Coxa 1 not noticeably shorter than 2, hind corner with 2 cusps. Coxae 2-3 with 2-3 hind cusps. Coxa 4 relatively broad, hind process curved upwards. Gnathopod 1, basis weakly setose; carpus stronger than propod, dactyl stout,

overhanging short, vertical palm. Gnathopod 2, basis nearly bare; propod rectangular, slightly longer than carpus, dactyl overhanging short vertical palm, hind margin with 2 groups of setae.

Peraeopods 3 & 4, hind margins of segment 4-6 with regular spines, dactyl finely pectinate behind. Peraeopods 5-7 irregularly homopodous, bases unevenly expanded, hind margins nearly straight, 6 relatively narrow, 7 broadest, hind lobes deep; segment 4 broad; segment 5 short, 6 relatively long; dactyls thick, anterior margins very finely pectinate.

Pleon plate 3 hind corner strongly produced acuminate. Uropods relatively stout, rami short, broad, especially outer ramus, much shorter than peduncle, margins weakly spinose. Uropod 3, inner ramus, margins each with 3 spines; outer ramus, outer margin with 2 spines, inner margin bar. Telson medium short, length 1.7 X width, apex evenly rounded.

Distribution. Ariake Sea (1 specimen only).

Taxonomic commentary. *Dactylopleustes obsolescens* is clearly distinct from *echinoicus*, but more closely similar to *echinoides*. It is distinctive in the unlike form of peraeopods 5-7, the short, weakly armed uropods, and the very elongate mandibular palp segment 3.

Pleusirinae Bousfield & Hendrycks, 1994

Pleustidae Gurjanova 1972: 135, 138 (key) (part).—Barnard & Karaman, 1991: 649.

Pleusirinae Bousfield & Hendrycks, 1994: 40.

Type genus. *Pleusirus* Barnard, 1969b, original description.

Diagnosis. Body small, slender, dorsally smooth; urosome 2 occluded dorsally. Head, rostrum short, deflexed, anterior head lobe broadly rounded. Eye rounded. Antennae slender, medium, antenna 1 the longer. Antenna 1, peduncles 2 & 3 short; accessory flagellum minute, apex setose; antenna 2, peduncle medium strong.

Mouthparts strongly modified. Upper lip broad, lobes asymmetrical. Lower lip, inner lobes deep, narrow. Mandible, molar reduced to a large smooth lobe; spine row short, blades short; left lacinia multi-dentate (9-10); right lacinia lacking; palp slender, segment 2 longest; segment 3 shorter, lacking baso-facial seta; segment 1 elongate. Maxilla 1, inner plate small, bare; outer plate with 9 apical spines; palp slender, facially pilose, apex weakly armed. Maxilla 2, plates small, weakly setose-spinose. Maxilliped, inner plate short, with few apical and inner marginal spines; outer plate narrow, columnar; palp large, subcheliform; segment 3 widest medially, not produced beyond base of slender dactyl.

Coxal plates 1-4 increasing in size posteriorly, rounded below, lacking hind cusps. Gnathopods 1 & 2 slender, subequal, "eusiroidean" in form, not sexually dimorphic;

carpus elongate, hind lobe shallow; propod subovate, palm long, lacking median tooth; posterior angle with 2 spine clusters.

Peraeopods 3-7 slender; dactyls short. Peraeopods 5-7 closely homopodous in size and form; bases broad, rounded behind; segment 4 little overhanging segment 5 behind.

Pleon plates 1-3, hind corners acuminate. Pleopods strong, not sexually dimorphic. Uropods 1-3 slender, rami elongate, spinose. Telson elongate, keeled proximally, pemicillate setae median.

Coxal gills narrow, saclike on peraeopods 2 & 3, plate-like on peraeopods 4-6, increasing posteriorly.

Taxonomic commentary. The subfamily appears allied with the subfamily Parapleustinae in most character states, especially of the mouthparts. It is unique in the eusiroidean form of the gnathopods, the generally reduced form of maxillae 1 & 2, the inflated, distally smooth mandibular molar; elongate mandibular palp segment 1; and the semi-subchelate form of the maxilliped palp.

Pleusirus J. L. Barnard

Pleusirus J. L. Barnard, 1969b: 204.—Gurjanova, 1972: 135.—Barnard & Karaman, 1991: 649.

Type species. *Pleusirus securrus* Barnard, 1969b: 204.

Subspecies. *Pleusirus securrus asiaticus* Kudrjaschov & Tzvetkova, 1975, original designation.

Diagnosis. With the characters of the subfamily, and in addition: Antenna 1, peduncular segment 1 with postero-distal process; flagellar segments, posterior marginal aesthetascs paired, prominent.

Mandibular blades thick, distally pectinate; incisor 7-8-dentate, third tooth largest. Maxilla 1, palp segment 1 with "shoulder" seta. Maxilla 2, inner plate not broadened, lacking inner marginal plumose seta. Maxilliped, inner plate with stout inner marginal and apical spines.

Gnathopods 1 & 2, bases slender, margins not strongly setose; propod, hind margin smooth; dactyl slender.

Peraeopods 5-7, coxae deep, postero-lobate, hind lobes rounded, segment 5 not longer than 4.

Uropods 1 & 2, inner ramus longer than peduncle. Uropods 2 & 3, outer ramus short. Telson rounded, penicillate setae median.

Male: Antennal segments with prominent aesthetascs; peraeopods 5-7 relatively slender; dactyls relatively long, slender, nearly straight.

Taxonomic and distributional commentary. The genus encompasses two forms, one a subspecies of the other, one on the Asiatic and the other on the North American Pacific coast.

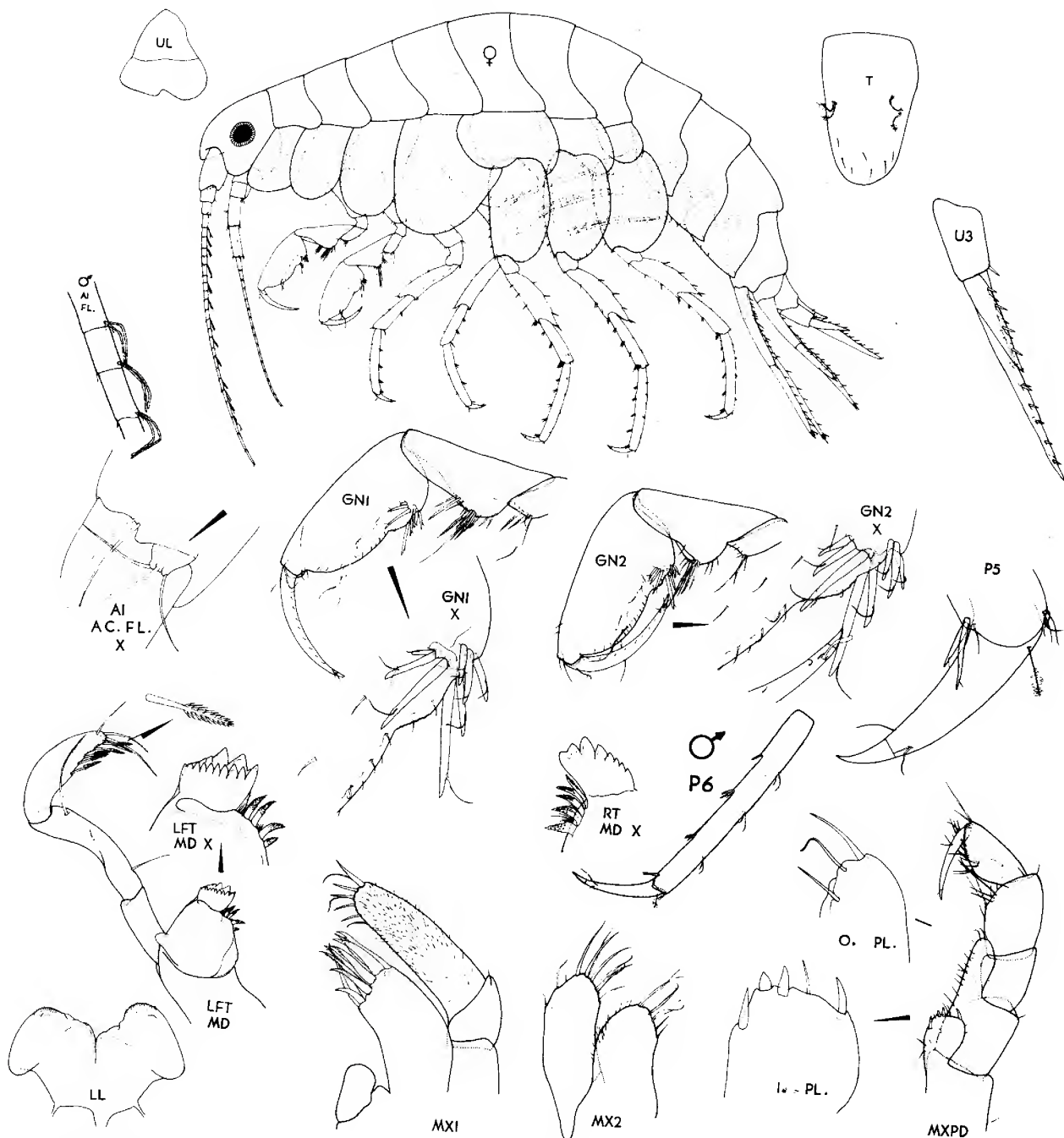


FIG. 42. *Pleusirus secorrus* Barnard. Female (3.7 mm); male (2.1 mm). Wickaninnish Bay, B.C.

Pleusirus secorrus J. L. Barnard
(Fig. 42)

A125 (1); A129 (1); A131 (5); A139 (2); A147 (4); A151 (2);
A164 (3); A168 (1); A171 (4); A175 (7).

Pleusirus secorrus J. L. Barnard, 1969b: 204, fig. 56.—
Gurjanova, 1972: 135, 138 (key).—Austin, 1985: 592.—
Staude, 1987: 379.—Barnard & Karaman, 1991: 650.

Material examined.

ALASKA. 46 specimens (all females, a few subadults) from
18 localities, as follows:

Southeastern Alaska: ELB Stns., June-July, 1961: A3 (8);
A6 (12); A8 (1); A48 (1); A75 (3); A80 (7); A81 (1); A92 (6);

BRITISH COLUMBIA. 252 specimens (including 1 male?)
at 59 localities, as follows:

Queen Charlotte Islands. ELB Stns., July-Aug., 1957: H14
(2); W4a (2); W4b (3); E5 (1); E25 (1); W8 (7); W9 (1); W11
(7); W12a (3).

Northcentral coast. ELB Stns., July, 1964: H1 (15); H3 (2);
H5 (30); H7 (12); H8 (2); H10 (2); H12 (8); H26 (5); H23
(1); H29 (1); H30 (10); H47 (1); H48 (2); H50 (3); H53 (20+);
H57 (1); H65 (6). ELB Stn., 1959: N22 (2).

Vancouver Island, north end: ELB Stns., July, 1959: O1 (1); O5 (3); O11 (3); O13 (7); O15 (7); V5 (2); V7 (3); V11 (1); V17 (2); V18 (1); N 11 (1); N16 (1).

Vancouver Island, south end: ELB Stns., July-Aug., 1955: F1 (6); F4 (1); P2 (1); P7 (1). ELB Stns., 1970: P715 (1); P716 (2); P718 (13); P719 (1). ELB Stns., 1975: P5b (2); P5c (1); (20) (4). ELB Stns., 1976: B3 (2); B4 (2); B5 (1); B7 (10). ELB Stns., 1977: B7a (8); B11b (1); B14 (1); B19b (2); B21b (3). ELB Stn. O15, Box I., Wickaninnish Bay, in *Phyllospadix* clumps, algal mats, over bedrock, LW level, Aug. 16, 1959 - female ov (3.7 mm) (slide mount) (fig'd specimen) + 7 other females.

Duncan Bay, Middle Pt., barge, 3-4 m dive, *Ulva* & bryozoans, P. Shaw coll., Seot 5, 1987 - 1 male (fig'd) + 6 specimens.

WASHINGTON-OREGON. 22 specimens at 3 localities, as follows:

Coastal localities: ELB Stns, July-Aug., 1966: W40 (18); W42 (2); W58 (2).

Diagnosis. With the characters of the genus and subfamily. The subspecies *asiaticus* Khudrjashov & Tzvetkova, 1975, may prove to be morphologically, if not ecologically, distinct, but western Pacific material was not re-examined in this study.

Distributional ecology. On the North American Pacific coast this species occurs from southeastern Alaska, through British Columbia, Washington and Oregon, to southern California. It occurs commonly from the extreme LW level to depths of 25 m, in clumps of *Phyllospadix*, algae, and in organic debris, often on shelly sand bottoms, mainly at cold, high salinity, outer coast locations.

***Pleusirus secorrus asiaticus* Kudrjashov & Tzvetkova**

Pleusirus secorrus asiaticus Kudrjashov & Tzvetkova, 1975: 1314, fig. 2A.—Tzvetkova & Kudryashov, 1985: 1.

Pleusirus secorrus Ishimaru, 1985d: 103.—Ishimaru, 1994: 54.

Taxonomic and distributional commentary. This form was collected from clumps of algae and *Phyllospadix* at stations on South Sakhalin I., in the southern part of the Sea of Okhotsk, and south to Pos'yey Bay in the Sea of Japan. It is also recorded from amongst fronds of *Tichocarpus carinatus*, *Cytoseira* sp., and *Laminaria japonica*. Females with eggs and early juveniles occur in July and August.

The Asiatic form of *P. secorrus* has been synonymized by Ishimaru (loc. cit.) and Barnard & Karaman (loc. cit.). However, taxonomic differences noted in the original description (Kudrjashov & Tzvetkova, loc. cit.) suggest that a different species may be involved. In order to justify recognition of *asiaticus* as a full species, it is recommended that the original material be re-examined, redescribed and fully figured.

Systematic and Biogeographical Analyses

This study treats the systematics and distributional ecology of 29 species of the gammaridean subfamily Parapleustinae that occur along both Asiatic and North American coasts of the North Pacific region. A modified phenetic cluster analysis, and corresponding cladistic analysis, indicated the Parapleustinae to be the most advanced phyletically of the 12 recognized subfamilies within family Pleustidae (Bousfield & Hendrycks, 1994). We conclude here by commenting in greater detail on aspects of the morphology and lifestyle and on biogeographical relationships of its component genera and species.

The seven genera of Parapleustinae appear similar in the overall plesiomorphic form of the body and appendages. Greatest morphological diversity occurs in the numbers and kinds of mandibular blades, in the cutting edges of the incisors and left lacinia, and to lesser extent in the form and armature of the gnathopods. Sexually dimorphic gnathopods occur, uniquely in this subfamily, among the Pleustidae. The taxonomic and phyletic relationships of the seven genera are not readily apparent through general inspection, but may be clarified through numerical analysis of characters and character states of those body features (Fig. 43, page 127). For this purpose, a modification of the UPGMA cluster analysis system of Sneath and Sokal (1973) is utilized. The 20 selected taxonomic characters and corresponding character states are outlined in Table I. The overall degree of evolutionary advancement of the genus is provided by a plesio-apomorphic (P.-A.) index, derived by summing the values for each character state for each species, as explained in previous analyses (e.g. Bousfield and Hendrycks, 1994; Jarrett & Bousfield, 1994).

The phenogram of morphological relationships (Fig. 43) suggests that the seven genera are not very closely similar, at least in the characters considered. Only two generic pairs, the North American endemic *Gnathopleustes-Trachypleustes*, and the broadly temperate-subtropical *Incisocallope-Commensipleustes* cluster at similarities of 70% or better. The pan-Pacific genera *Micropleustes* and *Parapleustes* cluster at 60-65% with the latter complex. However, the mainly North American genus *Chromopleustes* stands in isolation, with less than 50% similarity to the other generic groupings. The P.-A. index is slightly less than 20 (less than 50% of maximum apomorphy) for all genera except the relatively advanced genus *Incisocallope* where the value is 30 (75% of maximum). These values may indicate that the members of the Parapleustinae are evolutionary "stable", i. e., they remain "locked in" to exploitation of specialized shoal-water niches (e.g., within *Phyllospadix* communities) of the North Pacific region that either do not exist elsewhere (e.g., in the cold-temperate North Atlantic or antiboreal regions), or else are inaccessible because of past and present physical and physiological barriers to dispersal.

A phenogram of morphological relationships within species of the genus *Incisocallope* is provided in Figure 44,

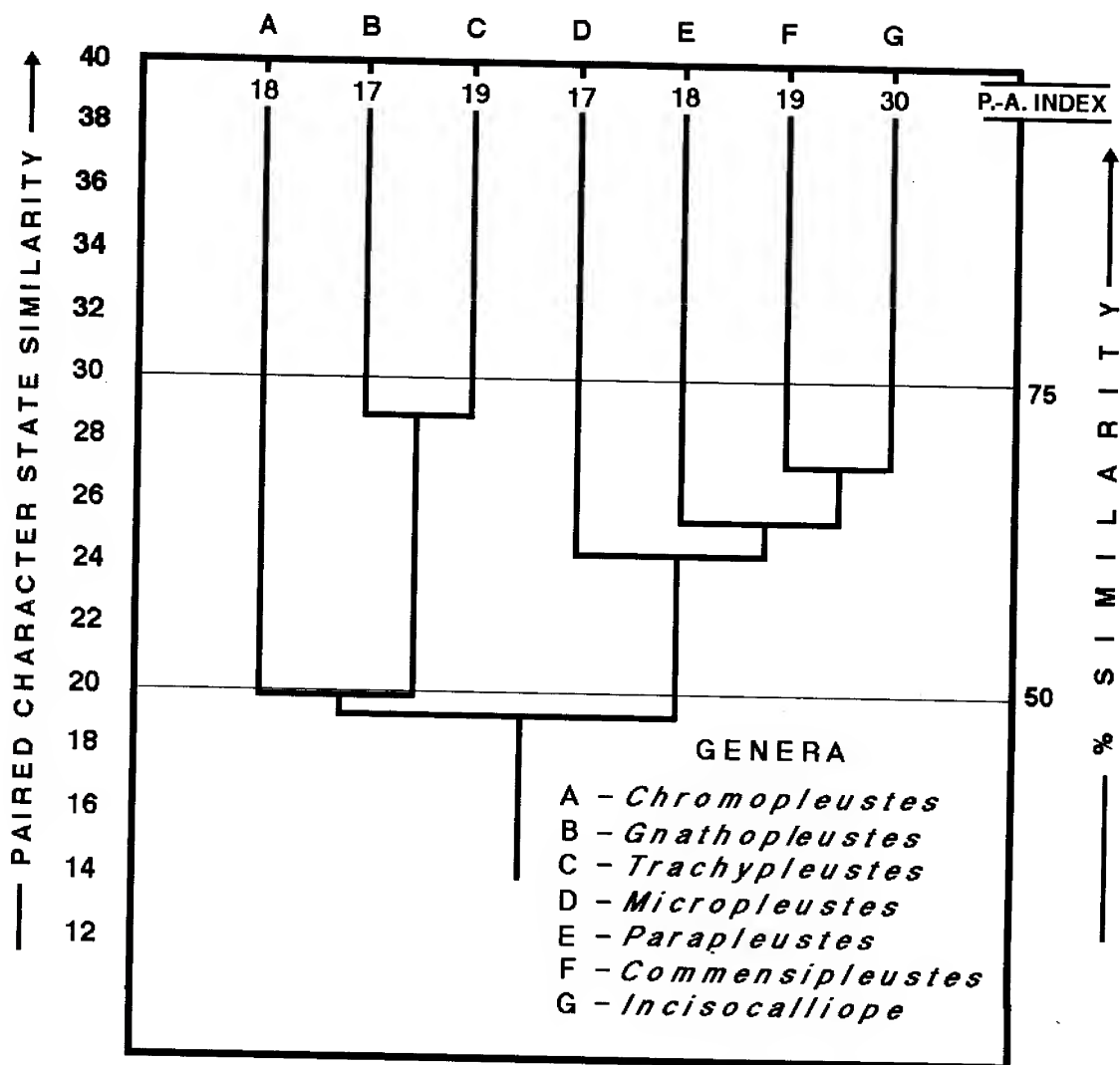


FIG. 43. PHENOGRAM OF GENERA OF SUBFAMILY PARAPLEUSTINAE

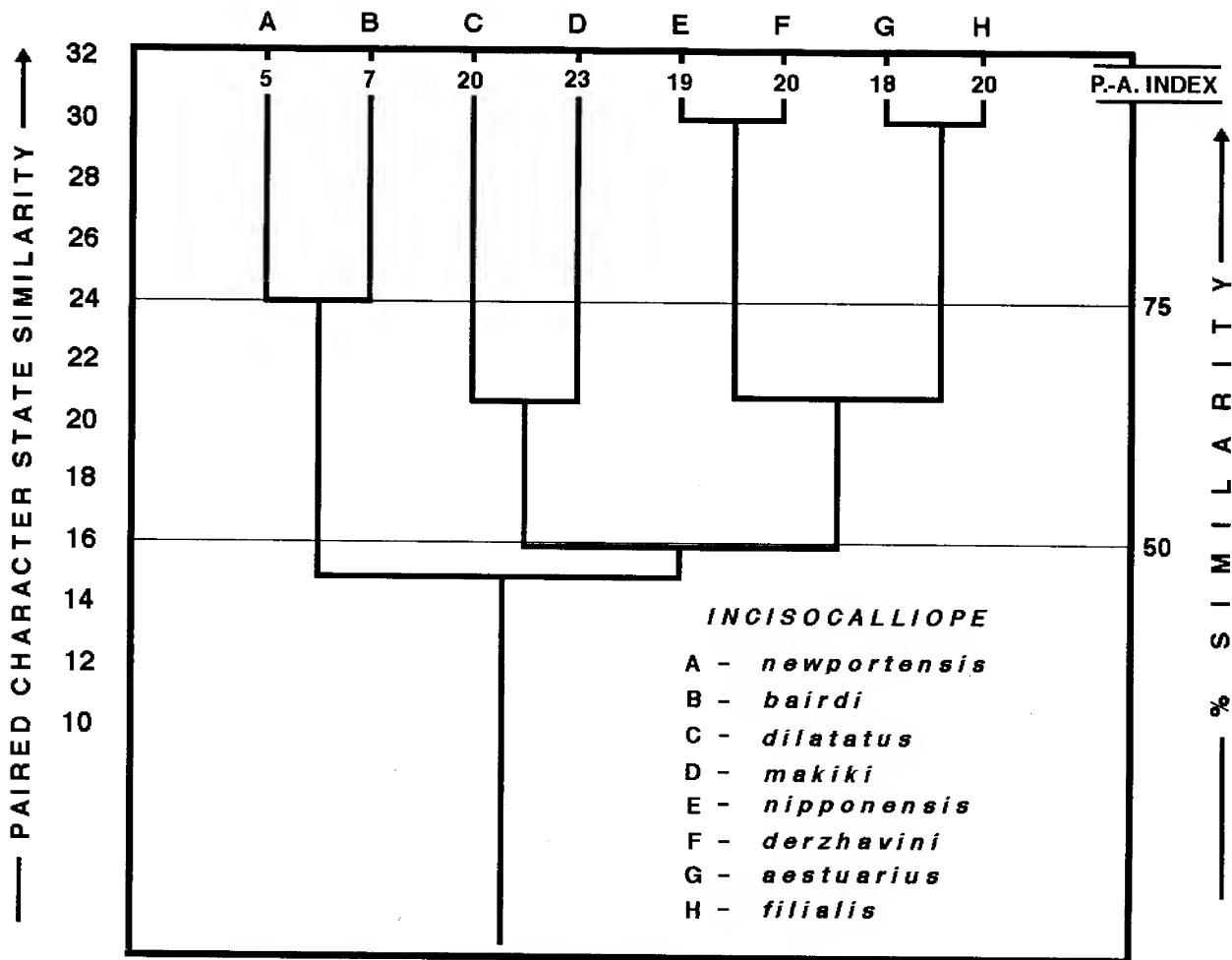
p. 129. The analysis is based on 16 characters and corresponding character states provided in Table II, p. 130. The 8 species cluster into three main assemblages at similarities of 65-75%, viz., a relatively primitive *newportensis-bairdi* group, a very advanced *dilatatus-makiki* group, and a slightly less advanced *derzhavini-aestuarius* group of two closely similar species pairs. These three major assemblages cluster at about the 50% similarity level and appear therefore not closely related. The *newportensis-bairdi* subgroup, known only from inshore waters of southern California, is especially plesiomorphic in character states of the mouthparts and pereopods, but the gnathopods are powerfully subchelate, and relatively advanced.

Possible biogeographical relationships of the *dilatatus-makiki* group are discussed below (pp. 129-30). The close similarity of the regionally co-occurring sibling species pair of *derzhavini* and *nipponensis* is not unexpected. However, the 90% morphological similarity between the widely separated Asiatic Pacific *filialis*, and the North American Atlantic *aestuarius* is unexpected and defies ready explanation.

Similar analysis of the North American endemic genus *Gnathopleustes* suggests that *G. pugettensis*, *G. simplex*, *G. pachychaetus* and *G. den* form a relatively advanced and closely related species complex that collectively have a continuous distribution from southeastern Alaska to southern California (Table II, p. 129). *Gnathopleustes trichodus* and *G. serratus* are relatively primitive morphologically, isolated phylogenetically and more restricted distributionally. The *Trachypleustes* species complex, with highly modified mandibular blades, and possibly more speciose than here considered, is more northerly in distribution. At least one species attains the Bering Sea region but has not yet been taken on the Asiatic coast. The *Micropleustes* complex is more speciose on the Asiatic coast. However, the most common North American species of this genus, *M. nautilus*, has the widest range of any parapleustine in the North American Pacific region, from the Bering Sea to southern California. With respect to subfamily Pleusirinae, *Pleusirus securus*, including its Asiatic subspecies, is the only known member of family Pleustidae to occur in all nine biogeographic zones of the North Pacific region. Subfamily Dactylopleustinae is

TABLE I. CHARACTERS AND CHARACTER STATES: GENERA OF PARAPLEUSTINAE

CHARACTERS	CHARACTER STATES		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Antenna 1, peduncular segment 2: segment 1	long		short
2. Antenna 2, peduncular segments 4 & 5	long		short
3. Upper lip, lobes	shallow subequal		deep, markedly asymmetrical
4. Lower lip, inner lobes	deep narrow		shallow broad
5. Mandibular blades	numerous (>10) long, slender	(7-8) short, acute	few (~5) short, flat
6. Mandible, palp segment 3, number of "D" spines	12-15	8-10	~5
7. Mandibular left lacinia, number of teeth	5-6	7-9	10+
8. Maxilla 1, outer plate, number of apical spines	9	11	15+
9. Maxilla 1, palp segment 1, number of setae	0	1	2
10. Maxilla 2, width of inner plate	narrow L>W		broad, L=W
11. Maxilliped, inner plate, number facial setae	7-10		0 - 2
12. Maxilliped, segment 3	short		large
13. Gnathopods 1 & 2, size of propod	weak shallow		strong deep
14. Gnathopods 1 & 2, size of carpus	elongate shallow		short deep
15. Gnathopods 1 & 2, degree of sexual dimorphism	none		marked
16. Gnathopods 1 & 2, palmar tooth	strong	vestigial	lacking
17. Coxae 1-3, number of posterior marginal spines	none		3-4
18. Peraeopods 3-7, size of segment 5: segment 4	subequal		5 distinctly shorter
19. Uropods 1 & 2, ramal spines	numerous strong		few weak
20. Telson shape	short broad		elongate narrow

FIG. 44. PHENOGRAM OF SPECIES OF *INCISOCALLIOPE*

represented on Asiatic and North American coasts by the species pair of *Dactylopleustes obsolescens* and *D. echinoides*, respectively. Although these echinoid-commensal species probably have geographical ranges similar to their host species of *Strongylocentrotus*, locality records are yet insufficient for meaningful biogeographical analysis.

Biogeographical considerations

The subfamily Parapleustinae is essentially endemic to continental coasts of the North Pacific region (Table III, p. 131). The distribution of five of the seven genera (i.e. *Chromopleustes*, *Micropleustes*, *Gnathopleustes*, *Trachypleustes* and *Commensipleustes*) is essentially cold-temperate, whereas *Parapleustes* is subarctic-boreal, and *Incisocalliope* is temperate-subtropical. Of its 28 described species here included, only three species have been recorded elsewhere, viz., *Parapleustes gracilis* from arctic-subarctic, marine parts of the North Atlantic and western Arctic Oceans; *Incisocalliope aestuarius* from temperate estuaries of the western North Atlantic, and *I. makiki* from the Hawaiian Islands in the south-central subtropical North Pacific.

In the northern North Pacific region, 16 species of

parapleustins, representative of all seven genera, occur along the coasts of continental North America, whereas only nine species, in four genera, have been recorded to date from the Asiatic continental coast (Table III). In the eastern North Pacific, species numbers are largest along the coast of British Columbia (10 species in each of zones 5, 6) but decrease both northwards and southwards. In the western North Pacific, the fauna of the Asiatic coast is less well known, but most (7) parapleustin species occur in the northern part of the sea of Japan, and fewer (3) in the cold waters of the Sea of Okhotsk to the north. Although no single species has yet been recorded from both continental coasts, the Bering Sea contains five species in four genera, and presumably provides the major pathway of gene flow between the two continental populations.

However, North American species of *Incisocalliope* (i.e. *newportensis* and *bairdi*) are widely separated from their Asiatic counterparts (e.g. *filialis*, *derzhavini*, *nipponensis* and *dilatatus*) and are relatively primitive morphologically (Fig. 44, above). These facts would suggest that these populations have been separated geographically for a considerable time, perhaps since the early Palaeogene (50-60 m.y.b.p.) when northern Pacific sea levels were lower, and marine climates were warmer and more equable (Adams,

TABLE II. CHARACTERS AND CHARACTER STATES: *INCISOCALLIOPE* SPECIES

CHARACTER	CHARACTER STATE		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Antenna 1, number flagellar segments	30+	~25	<15
2. Antenna 2, number flagellar segments	20+	10-15	~5
3. Mandible, palp seg. 3, number "D" setae	~10		~5
4. Mandible, number of blades in row	10		5
5. Maxilla 1, palp 2, number facial setae	4		0
6. Maxilliped, inner pl., apical "button" spines	4+	3	2
7. Gnathopod 1, basis, ant. marginal setation	nearly bare		strong throughout
8. Gnathopod 1, carpal lobe	broad shallow		narrow deep
9. Gnathopod 1, posterior margin, no. setal gps.	3		0
10. Peraeopods 3 & 4, segment 5: segment 4	subequal		markedly shorter
11. Peraeopods 5-7, width of basis	broad		narrow
12. Peraeopods 5-7 hind lobe depth	width~depth deep, reaching segment 4		width<< depth shallow
13. Uropod 1, peduncle outer marginal spines	numerous (10+)		few (4) basal position
14. Uropod 2, length of outer ramus: inner	long subequal		markedly shorter
15. Uropod 3, length of outer ramus: inner	long (75%+)		short (~60%)
16. Telson, rel. form	long, slender		short, broad

1981). During that period, and perhaps later, early members of the genus may have penetrated via a southern waterway (now blocked by the Panamanian isthmus) to the western Atlantic region where *Incisocalliope aestuarius* remains a sole survivor. The widely disjunct distributions of the *filialis-aestuarius* species pair is also reminiscent of somewhat similar disjunct distributions of the coastal aquatic arachnid order Xiphosurida (Savory, 1964), and the coastal aquatic reptilian genus *Alligator* (Carr, 1963). Both these groups may have been biogeographically continuous between southern Asia and North America during early to middle Cretaceous times, via a Tethyan marine pathway outlined by Howarth (1991). Such a hypothesis is unlikely for parapelestins and related subfamily members of which no relict modern representatives now exist along that route and/or are physiologically unsuited to those marine thermal regimes. The presence in the remote Hawaiian islands of *Incisocalliope makiki*, closely related to *I. dilatatus* of the Asiatic group,

is anomalous. However, *I. makiki* may prove to be a relict species, representative of an ancestral group from Japan that penetrated the Hawaiian Archipelago, perhaps during the early Tertiary. They may have survived by "island hopping" as the volcanic islands of the chain successively emerged in the east and eroded away in the west (Howarth & Mull, 1992).

In summary, subfamily Parapelestinae encompasses diverse, relatively advanced morphotypes and specialized lifestyles of pleustid micropredators. These occupy various niches within the *Phyllospadix* and sessile invertebrate communities of intertidal and shallow water habitats, almost exclusively within the North Pacific region. Although this fauna is believed relatively ancient, and probably originated during Mesozoic times (Bousfield, 1982b), the long-term stability of regional shallow-water ecosystems and their marine climates may have been major factors in dampening evolutionary thrust in other directions.

**TABLE III . DISTRIBUTION OF GENERA AND SPECIES OF PARAPLEUSTINAE
IN THE NORTH PACIFIC REGION.**

TAXON	B I O G E O G R A P H I C Z O N E								
	1	2	3	4	5	6	7	8	9
1. <i>Chromopleustes</i> <i>C. johanseni</i> <i>C. oculatus</i> <i>C. lineatus</i>		X	x X	X x	X X	x X	x		
2. <i>Micropleustes</i> <i>longimanus</i> <i>behningioides</i> <i>behningi</i> <i>nautilus</i> <i>nautiloides</i>	X X X	x		X	X	X x	X X	X x?	x
3. <i>Parapleustes</i> <i>ishimarui</i> <i>americanus</i> <i>gracilis</i> *		x	X	X	X	x			
4. <i>Gnathopleustes</i> <i>serratus</i> <i>pachychaetus</i> <i>trichodus</i> <i>simplex</i> <i>pugettensis</i> <i>den</i>				X X x	X X x X	X X	X X	x X x	 ? X
5. <i>Trachypleustes</i> <i>trevori</i> (+ varieties) <i>vancouverensis</i>			x	x	X	X x	?		
6. <i>Commensipleustes</i> <i>commensalis</i>								?	X
7. <i>Incisocalliope</i> <i>filialis</i> <i>derzhavini</i> <i>nipponensis</i> <i>dilatatis</i> <i>makiki</i> ! <i>newportensis</i> <i>bairdi</i> <i>aestuarius</i> +	X X X X								 X X

* N. Atlantic-subarctic; ! Hawaiian Islands; + N. American Atlantic temperate

BIOGEOGRAPHIC ZONES:

1. Sea of Japan; 2. Sea of Okhotsk; 3. Bering sea and Aleutians; 4. Southeastern Alaska; 5. Northern B. C.; 6. Southern B. C.; 7. Wash.-Oregon; 8. Northern California; 9. Southern & Baja California.

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LEGEND FOR FIGURES

A1	- antenna 1	MX 1	- maxilla 1
A2	- antenna 2	MX2	- maxilla 2
AC FL	- accessory flagellum		
BR.	- coxal gill	MXPD	- maxilliped
BR PL	- brood plate	O. P.	- outer plate
CX	- coxal plate(s)	P3-P7	- peraeopods 3-7
DACT	- dactyl	PLEOS	- pleosome
DORS	- dorsal view	PLP	- palp
EP 1-3	- pleon plates 1-3	RT	- right
GN1	- gnathopod 1	SET	- seta(e)
GN2	- gnathopod 2	SP	- spine
HD	- head	T	- telson
I. P.	- inner plate	U1-U3	- uropods 1-3
I. R.	- inner ramus	UROS	- urosome
LFT	- left	X	- magnified
LL	- lower lip	♂	- male
MD	- mandible	♀	- female

Additions to Amphipacifica, Vol. I(4), 1995.

The following catalogue numbers have been provided through the courtesy of the Invertebrate Curatorial Unit, Canadian Museum of Nature, Ottawa, pertinent to the following paper:

Bousfield, E. L., & E. A. Hendrycks, 1995. The amphipod superfamily Eusiroidea in the North American Pacific Region. I. Family Eusiridae: systematics and distributional ecology. *Amphipacifica* I (4): 3-59.

1. *Eusirus columbianus* Bousfield & Hendrycks, 1995, pp. 10-11, fig. 5.

Female (5.2 mm), **Holotype** (slide mount). CMN Cat. no. NMCC1995-0001.

2. *Rhachotropis calceolata* Bousfield & Hendrycks, 1995, pp. 26-27, fig. 16.

Female ov (8.7 mm), **Holotype** (slide mount). CMN Cat. no. NMCC1995-0005.

3. *Rhachotropis boreopacifica* Bousfield & Hendrycks, 1995, p. 29, fig. 17.

Female br. I (10.5 mm), **Holotype** (slide mount). CMN Cat. no. NMCC1995-0006.

Female (unspecified), **Paratype**. CMN Cat. no. NMCC1995-0007.

4. *Rhachotropis minuta* Bousfield & Hendrycks, 1995, p. 35, fig. 22.

Female ov (3.8 mm), **Holotype** (slide mount). CMN Cat. no. NMCC1995-0008.

2 other females, ELB Stn. P3, West Bay, B. C., Nov. 2, 1977, **Paratypes**. CMN Cat. no. NMCC1995-0009.

5. *Rhachotropis conlanae* Bousfield & Hendrycks, 1995, p. 37, fig. 23.

Female (4.5 mm), **Holotype** (slide mount). CMN Cat. no. NMCC1995-0010.

Female (4.1 mm), Boca de Quadra, southeastern Alaska, June 27, 1989, **Paratype**. CMN Cat. no. NMCC1995-0011.

Catalogue numbers remain pending for the following species:

1. *Eusirus hirayamae* Bousfield & Hendrycks, 1995, p. 10, fig. 3.

Male (6.5 mm), **Holotype**. Ariake Sea, Japan.

Original material described and figured (as *E. longipes* Boeck) in: Hirayama, A., 1985. Publ. Seto Mar. Biol. Lab. 30: 29, figs. 142-147. Collections of the Amakusa Marine Biological Laboratory (AMBL), Amakusa, Japan.

2. *Cleonardo moirae* Bousfield & Hendrycks, 1995, pp. 15-17, fig. 7.

Female ov. (7.0 mm), **Holotype**. Institute of Ocean Sciences (IOS), Sidney, B. C.

3. *Rhachotropis barnardi* Bousfield & Hendrycks, 1995, pp. 29-31, fig. 18.

Male (3.3 mm), **Holotype**. Unspecified **Paratypes**.

Original material briefly described and figured (as *R. clemens* Barnard) in: Barnard, J. L., 1971: Smiths. Contr. Zool. 61: 10, figs. 6, 7. Off Oregon, 200 m. Collections of the United States National Museum, Washington, D. C.

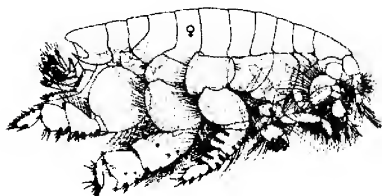
4. *Rhachotropis americana* Bousfield & Hendrycks, 1995, p. 40, fig. 26.

Female (11.3 mm), **Holotype** (slide mount); male (9.5 mm), **Allotype**; 5 females, 1 male, **Paratypes**. RBCM/CMN Stn. 91-1-119. Collections of the CMN, Ottawa.

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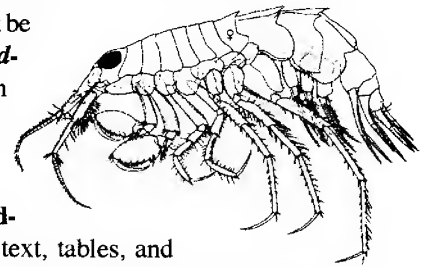
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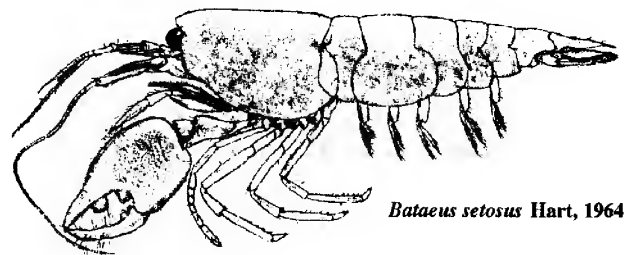
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